THE EVOLUTION OF UNUSUAL SHELL MORPHOLOGIES IN FOSSIL AND LIVING TURRITELLIDAE (GASTROPODA)

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By
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Abstract –

Unusual morphologies are apparently novel forms or features, representing large increases in disparity within a clade. Turritellid gastropods are a Jurassic-Recent group of marine snails, with ~140 valid, named living species and ~800 valid fossil species. They are often the dominant macrofaunal in assemblages in which they occur, and are important for biostratigraphy and paleoclimatology. The unusual morphologies investigated in this study are uncoiling, occurring in the *Vermicularia*, and septation, which has been considered characteristic of the family Turritellidae, but unusual among gastropods as a whole.

In chapter one, I construct a global molecular phylogeny for turritellids. Turritellids have notoriously simple shells, inhibiting understanding of supraspecific relationships among species and the widespread adoption of most proposed generic names. We constructed a molecular phylogeny of more than 30 species from a globally distributed dataset based on the 12S and 16S mitochondrial and nuclear H3 regions. Several distinct clades were recovered, with molecular distances indicating divergence times were likely older than the Miocene. A generic revision is proposed.

In chapter two, I construct both molecular and morphological trees for fossil and Recent members of the Miocene-Recent group *Vermicularia* (Cerithioidea: Turritellidae).

We provide a revised taxonomy with more detailed diagnoses for all known living and fossil species. A new species is described from the early Pliocene from the Dominican Republic.

In chapter three, I examine the evolution of the *Vermicularia* in an evolutionary developmental biology framework. Isotopic sclerochronology was used to determine growth patterns and rates in both fossil and Recent species within the phylogenetic framework established in chapter two. This ontogenetic information allows study of the specific heterochronic mechanisms involved in the origin of these species' morphologies.

In chapter four, I demonstrate that septation in turritellids is not an anomaly, but is a widespread feature of high-spired gastropods. Adaptive hypotheses for turritellid septation do not survive strong scrutiny. I outline a methodology for testing the hypothesis that a feature originated as a spandrel, rather than the direct product of selection for that feature. I conclude that septa within turritellids are spandrels of shell thickening, rather than being adaptive themselves.

BIOGRAPHICAL SKETCH

Brendan Anderson completed his B.A. at Dartmouth College in Biological Sciences and Religion in 2009, and his M.S. in Geology at the University of Kansas in 2013.

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Chapter 1: A molecular phylogeny of Turritellidae (Cerithioidea), including biogeography and generic revision

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Abstract— Turritellidae is a globally distributed, Jurassic-Recent family of cerithioidean gastropods. They have notoriously simple shells, inhibiting understanding of supraspecific relationships among species and the widespread adoption of most proposed generic names (Beu, 2010). We constructed a molecular phylogeny of more than 30 species from a globally distributed dataset based on the 12S and 16S mitochondrial and nuclear H3 regions. Parsimony, maximum likelihood, and Bayesian methods all yielded highly similar trees with several distinct clades with molecular distances indicating divergence times were likely older than the Miocene. Some of these correspond to the previously recognized genera or subgenera *Mesalia*, *Colpospira*, *Kurosioia*, *Maoricolpus*, *Neohaustator*, *Protoma, Turritella* s.s., *Vermicularia*, and *Zaria*. The remaining species, all previously assigned to "*Turritella* s.l." represent 4 clades which are assigned new generic names herein – *Aghuilhasturritella*, *Antonturritella*, *Paciturritella*, and *Tethyturritella*. The subfamily "Turritellinae" as generally used is paraphyletic, and we propose simplifying subfamilial organization by eliminating those included within a monophyletic Turritellinae (e.g. Vermiculariinae). Based on biogeographic relationships among taxa, turritellids do appear to have limited dispersal abilities as has long been suspected; only a few relationships indicate potential long-distance dispersal, with rare dispersal events by ocean currents likely significant in the origin of older clades.

Introduction

Turritelline gastropods are among the most abundant and widespread marine gastropod clades in both fossil and living marine communities since and are often the most abundant members of their communities (Allmon, 1988; 1996; 2007; 2011). The oldest known members of turritellinae (and possibly the oldest members of Turritellidae) are Oxfordian (Upper Jurassic) from western India (Das, Saha, Bardhan, Mallick & Allmon, 2018). Despite this modern and paleontological significance, their systematics remain notoriously problematic(Allmon, 2011). The most recent attempt at a comprehensive systematic review of Turritellidae (Marwick, 1957a) documented an abundance of generic and subgeneric names based on shell characters, but paleontologists and malacologists have been hesitant to adopt most without the support of molecular data (Allmon, 2011; Beu, 2010). The first molecular taxonomy of turritellidae was based on a partial 16S sequence in 10 taxa, primarily from the North America, and was notable for affirming *Vermicularia* as nested within Turritellinae (Lieberman, Allmon & Eldredge, 1993). The phylogeny developed here greatly expands taxonomic and biogeographic sampling and permits the assessment of the validity of a number of nominal genera.

Turritella is often considered an exemplary “wastebasket” taxon, especially for fossil species (Allmon, 1996; Hendricks et al., 2014; Plotnick & Wagner, 2006). The genus *Turritella* s.l. is often used for all members of the family (Allmon, 1996), and often species names are applied without taxonomic rigor, inflating geographic ranges. It has long been suspected that turritellids are subject to rampant convergence in gross shell morphology, especially whorl profile and adult spiral sculpture patterns (Allmon, 1992a; 1994; 1996; Beu, 2010; Kotaka, 1978), but also highly variable within species (Allmon, 1996; Das et al., 2018; Ryall & Vos, 2010). Key shell characters for defining many genera rely on the preservation of the protoconch (Allmon, 1992a; 1996; Garrard, 1972; Marwick, 1957a; 1957b), which is rare, even in live-collected specimens (Johnson, Anderson & Allmon, 2017), either due to characteristic protoconch morphology (Figure. S1.1) or to the order of appearance of the primary spiral cords (Figure. S1.2; A,B,C,D defined based on the position on the whorl as they first appear; see (Allmon, 1994; 1996; Beu, 2010; Marwick, 1957a). Despite these potential biases towards underestimating species diversity, turritellids remain among the most broadly distributed and diverse gastropod families – recent compilations estimate that there are perhaps 140 valid living species, with ⅓ to ½ of Recent species native to Australia (Beesley, Ross & Wells, 1998; Ryall & Vos, 2010), and ca. 800 valid fossil species (Allmon, 2011; Allmon & Smith, 2011; MolluscaBase, 2018). Supraspecific organization of turritellids remains confused (Allmon, 1992a; 2011; Beu, 2010; Hendricks et al., 2014).

This low taxonomic confidence inhibits studies of living and fossil diversity, extinction risk, and the evolutionary history of the group (Allmon, 1996). The inferred restricted dispersal ability of turritellines (based on the brief planktonic larval stage of most species; Beu 2010, (Sang et al., in review) has led workers on both recent and fossil species to presume that similar forms evolved independently in numerous parts of the world (e.g., (Marwick, 1957a), however this assumption requires reassessment utilizing molecular data to avoid circularity (Beu, 2010). Beu (2010) continues that “the family urgently requires a world-wide reassessment, and is another of the poorly understood families with few taxonomic criteria which would benefit greatly from a comparison of DNA sequences”.

Recent efforts (Anderson et al., 2018a; Sang et al., in review) have improved our understanding of relationships among neotropical American species, but here we present the first global molecular phylogeny of the family. By placing this phylogeny in biogeographic context we are able to assess the validity of the hypothesis that relationships among turritellines may generally be evaluated on a regional basis, an important assumption of many analyses of the evolutionary relationships among fossil turritellines (e.g., Allmon 1994; 1996).

Due to the systematic uncertainty inherent in assigning nearly all species in the family to *Turritella* s.l., ecological assessments based on the genus level particularly hazardous for this group. Beu (2010) noted that the world genus-level classification proposed by Marwick (1957a) “does little to resolve relationships within the family”. A revision of turritelline genera will permit genetic disparity in communities to be more easily evaluated by non-specialists, and can aid in prioritizing conservation decisions. Additionally, the recognition of major lineages among extant groups can provide insight into the relationships among fossil turritellines. Turritellines are at risk in the modern ocean due to pressures including invasive species, dredging, pollution, collecting for the shell trade, and habitat loss (Driessen & Hocking, 2008; Edgar, 2001; Göransson, 2002; Ng & Wee, 1994; Raut et al., 2005). A valid taxonomy is essential to evaluate regional and global biodiversity (Mace, 2004; Valdecasas & Camacho, 2003). Marine invertebrates are increasingly acknowledged to be under-studied and under-sampled systematically (Bouchet et al., 2002; Dayton, 2003; Gaston & May, 1992; Knowlton, 2000; Knowlton & Weigt, 1997; Kokko, 2017; Mace, 2004; Mikkelsen & Cracraft, 2001; Sala & Knowlton, 2006; Snelgrove, 2010), and poorly known groups have frequently proven to be more ecologically important than previously suspected (Valdecasas & Camacho, 2003).The IUCN red list appears to systematically underrepresent molluscan extinctions, due to differences in reporting and taxonomic effort, furthering the perception that marine molluscs are at less risk (Kokko, 2017; Regnier, Fontaine & Bouchet, 2009). Less than 3% of mollusk species have been assessed for conservation status, and although marine species may generally have lower extinction risk than terrestrial species, this is not true of all groups, and many taxa are likely to be at risk or become extinct without being recorded (Peters, et al., 2013; Regnier et al., 2009). At least one evolutionarily significant population of turritellines appears to have been extirpated before any conservation assessments were made (Anderson et al., 2018a; Anderson, Ivany & Allmon, 2018b).

Materials and Methods

Taxon Sampling

Our goal was to obtain as broad a sampling as possible of turritellid species, with an emphasis on biogeographically broad sampling and relationships among previously proposed genera. Live and/or appropriately preserved material is exceedingly difficult to obtain for most species. We were able to obtain sequence data for 60 individuals representing 33 species, including species that have been assigned to the genera *Colpospira*, *Kurosioia, Maoricolpus, Mesalia, Neohaustator*, *Protoma*, *Torcula*, *Turritella* s.s., *Vermicularia*, *Zaria*, and 17 species nominally placed in either “*Gazameda*” or “*Turritella* s.l.”. The majority of molluscan species are typically known from morphological shell characteristics only (Allmon & Smith, 2011; Bouchet & Strong, 2010; Páll-Gergely, 2017). This includes not only fossil taxa, but also species presumed to be extant. For example,“[a]fter 25 years of intensive exploration in New Caledonia, as many as 73% of the 1,409 turrid gastropod species documented are represented only by empty shells, and 34% by a single empty shell” (Bouchet, Lozouet & Sysoev, 2009), and this relationship holds for the less diverse turritellids as well. Additionally, several species of turritellid (and other molluscan taxa) which have been collected including the animal (notably many from the turritellid biodiversity hot-spot of Australia) have been formalin preserved, and are not amenable to sequencing (Jaksch et al., 2016; Páll-Gergely, 2017).

Sequence data was already available for several Western Atlantic and Tropical Eastern Pacific turritellids from projects seeking to understand changes in protoconch morphology (Sang et al., in review) and the relationship of *Vermicularia* to other turritellids (Anderson et al., 2018). New material sequenced for this study expands the biogeographic sampling considerably, especially for the western Indian Ocean and southwest Pacific. Specimens were provided by the Museum and Art Gallery of Northern Territory, Darwin, Australia (MAGNT); the KwaZulu-Natal Museum (NM), Pietermaritzburg, South Africa; the National Science Museum, Tokyo, Japan (NSMT); the Paleontological Research Institution (PRI), Ithaca, NY, USA; Smithsonian National Museum of Natural History (NMNH), Washington, D.C., USA; and the Tasmanian

Museum and Art Gallery (TMAG), Hobart, Tasmania, Australia. Specimens newly sequenced for this analysis are listed in Table 1.1.

Sequencing

Genomic DNA was extracted using the Qiagen DNeasy Kit from about 100 mg of tissue, following the manufacturer's protocol. Mitocondrial 16S, 12S, and nuclear histone H3 regions were sequenced as gastropod-specific primers were available for 16S and 12S (Simon, Franke & Martin, 1991; Zou, Li & Kong, 2011) and nonspecific H3 primers (Colgan et al., 1998) have been successful in other turritellids (Sang et al., in review; Anderson et al. 2018). Primer sequences used are available in table 1.2. The 16S region (527 bp) was amplified using the primers 16Sar and 16Sbr (Simon et al., 1991). The 12S region (456 bp) was amplified using the primars of Zou et al. (2011). The H3 region (376 bp) was amplified with the primers H3NF and H3NR of Colgan et al. (1998). Each PCR reaction consisted of 35 cycles of 95°C for 4.5 minutes, 95°C for 1 minute, 55°C for 1 minute, 72°C for 1:20 minutes, and 72°C for 4.5 minutes. 20µL PCR products were treated with 0.5µL exonuclease I (10U/µl) and 0.5µl shrimp alkaline phosphatase (1.0U/µl) at 37°C for 30 minutes, then at 90°C for 10 minutes. Sanger sequencing took place at the Cornell Biotechnology Resource Center.

Batillaria zonalis and *Lampania cumingi* (Batillariidae) were chosen as outgroup taxa based on their close relationship of Batillariidae to Turritellidae in combined morphological and molecular analysis of Strong et al. (2011). Sequence data was added to the alignment of Anderson et al. (2018), aligned with MUSCLE (Edgar, 2004), and visually checked using Mesquite v 3.40 (Maddison and Maddison, 2018).

Parsimony analysis of both molecular and morphological characters was performed in PAUP4 (Swofford, 2003). Likelihood analysis was performed using RAxML (Stamatakis, 2006) under a GTRGAMMA model to calculate the ML best tree and 100 bootstrap replicates. Trees were visualized on FigTree v. 1.4.3 (Rambaut, 2016). Bayesian analysis was performed using BEAST v1.8.0 (Drummond and Rambaut, 2007) with Batillariidae designated as a monophyletic outgroup, using 10 million generations, with the first 10% of results discarded as burn-in.

Genus Concept

Marwick (1957b), quoted in Allmon (1996), summarized generic assignments within Turritellidae:

> There has rarely been more reluctance to grant generic rank to subdivisions of a broad Lamarckian genus than there has been with *Turritella.* The main causes for the desire to retain Turritella as a world-wide, [Jurassic] to Recent genus are, no doubt, the small range in shape, the relatively simple aperture, and the general absence of well-developed axial sculpture. One rightly hesitates to grant generic significance to differences that seem trivial. When, however, such differences, on close study, emerge as reliable guides to what appear to be genetically related groups, their usefulness must not be ignored. Whether the subdivisions are accepted as genera, subgenera or sections, or neglected altogether, will depend on individual tastes, backgrounds and traditions. Much more information is needed about the animals themselves before a really satisfactory classification can be widely accepted (p. 7).

By reconstructing a phylogeny based exclusively on genetic characters we can provide information about the animals themselves, independent of shell characters, and determine a rational subfamilial organization for the group. It is our hope that in recognizing monophyletic lineages through molecular characters, new morphological characters uniting these groups may be found, similar to the revision of morphological characters considered important in coral systematics in light of molecular systematics (Budd et al., 2010; Fukami et al., 2004). Any definitively reliable characters or combinations of characters would allow the genus to then be recognizable when examined by those trained to look for these characters, even if they do not look dissimilar to the untrained (Allmon, 1992a; Marwick, 1957b; Reagan, 1925).

The frequent practice of assigning nearly all turritellids to "*Turritella* s.l." (Hendricks et al., 2014) does not convey substantial information about evolutionary relationships for a group with 160 million years of history and nearly 150 known living species. As Beu (2010) states, "clearly phylogenetic relationships in this family are expressed less than optimally if all species are placed in *Turritella*". Although a variety of species concepts are currently employed (e.g., De Queiroz, 2007; Nixon & Wheeler, 1990), it is generally agreed that species do correspond with biological realities (Allmon & Yacobucci, 2016; Garnett & Christidis, 2017; Hendricks et al., 2014; Villmoare, 2018). Genera in contrast are acknowledged to be constructed arbitrarily (Allmon, 1992a; Garbino, 2015; Hendricks, 2015; Hendricks et al., 2014; Villmoare, 2018) in order to convey information about biological organization. While some even argue that genera (and other higher taxa) can be used to convey ecological or morphological information exclusively (Lewin, 2001), we do not believe that taxonomic ranks should be erected which do not reflect evolutionary history (Greene, 2001; Hendricks et al., 2014). “Morphotypes” or ecological guild assignments can fulfill this role without intruding on the Linnaean hierarchy, and confusing the two may hinder the recognition of interesting episodes of convergence or parallelism. Therefore, we consider it inviolable that genera should be monophyletic (Dubois, 1982; Garbino, 2015; Hendricks et al., 2014; Hennig, 1965; 1966; Villmoare, 2018).

An important consideration is that if monophyletic genera are evolutionary individuals (Ghiselin, 1974; 2005; Hull, 1976; 1978), they are not well-behaved evolutionary individuals (Ghiselin, 2002; 2005; Hendricks et al., 2014), as monopohyletic genera are necessarily destroyed if they give rise to new genus level taxa (monophyletic genera could only be considered to reproduce other monophyletic genera when a new speciation event generates a species possessing such a highly derived morphology it necessitates the renaming of all lineages with the plesiomorphic character state). The concept of selection or sorting of genera based on reproduction and not differential extinction would favor clades that produced new, morphologically cryptic, species lineages frequently, but occasionally produce bizarre forms humans (Kokko, 2017) recognize as different. It is unclear if this would mean more for our understanding evolutionary theory or human psychology.

With the criterion of monophyly in mind, the subsequent consideration is how a taxon should be subdivided into genera, a “necessarily arbitrary task” (Garbino, 2015). From the perspective of utility, one additional criterion would be stability—genera should be well supported in phylogenetic analyses and unlikely to become obsolete as additional data or taxa are sampled (Garnett & Christidis, 2017; Hendricks, 2015;

Hendricks et al., 2014; Puillandre et al., 2014b). Another is that genera should convey some information about evolutionary history and relationship, therefore monotypic genera should only be erected if significant genetic distance (implying deep divergence time), or the monophyly of another, recognizable group necessitates it.

One, purely arbitrary, but widely proposed criterion is taxon age, often inferred from genetic distance (Garbino, 2015; Groves, 2004; Hendricks et al., 2014; Hennig, 1965; 1966; Puillandre et al., 2014b). While this does convey interesting information, especially regarding possible species sorting, it is absolutely tied to the snapshot perspective of modern civilization – in 5 million years new genera would need to be erected even if no new speciation or morphological change occurred. Nevertheless, this criterion is increasingly being employed in organizing molecular taxonomies of gastropod (Puillandre et al., 2014b) and other (Buckner et al., 2015; Garbino, 2015) clades. For gastropods (Conidae, Muricidae, Littorinidae), lineages with most recent common ancestors estimated to have been 10-55 million years before present are being recognized at the generic level (Castelin et al., 2012; Claremont et al., 2013; Puillandre et al., 2014b; Reid, Dyal & Williams, 2012). As most fossil species cannot be assigned to clades with any confidence at present, molecular clock estimates for internal nodes calibrated solely on the origin of non-Pareorine Turritellinae (Jurassic) and species presumed to be geminate pairs which diverged due to the closure of the Central American Seaway (Sang et al., in review) are unlikely to be precise. For Turritellidae, we do not seek to recognize groups with less genetic divergence from other clades than the recently evolved (Miocene ~ 15Ma), morphologically distinct genus *Vermicularia* from its sister lineage (Anderson et al. 2018a). By restricting the establishment of new generic names to lineages substantially more divergent than *Vermicularia* we are likely to avoid proposing genera substantially younger than those used in other gastropod groups.

An alternative criterion is ease of recognition – erecting genera based on groups that are highly morphologically or ecologically divergent (Allmon, 1992a; Garbino, 2015; Hendricks et al., 2014; Simpson, 1961). This criterion is particularly interesting from the perspective of macroevolutionary studies, which speak of "the origin of genera", but are most often truly interested in "the origin of highly derived lineages" (e.g., Allmon, 1992a; Anderson et al., 2018a; 2018b; Dubois, 1988; Lemen & Freeman, 1984; Stanley, 1978; Stanley, 1979). While some standard may be employed in a given study to define the degree of difference which establishes the boundaries of genera within a clade, these standards are also ultimately arbitrary (Villmoare, 2018). If morphologically or ecologically distinct clades are recognized and are sister to lineages retaining primitive characteristics, then a genus rank name is necessary for the plesiomorphic clade, or the criterion of monophyly would be violated (Hendricks et al., 2014). Monophyletic clades which are deeply divergent and recognizable on shell morphological criteria suitable for turritellids (e.g., unusual protoconch morphologies) should be adopted, even if they do not appear highly divergent to those not trained to refer to these criteria (Marwick, 1957b; Reagan, 1925).

Table 1.1. Specimen ID numbers for newly sequenced materials.

Species	Locality	Specimen ID No.	Genbank ID
accisa	Tasman Sea	TMAG 29209	BA23
alba/concave	Madagascar	NMNH ES8A02	ES8 A02
Banksia	Panama	NMNH ES1E06	ES1 E06
Banksia	Panama	NMNH ES1F06	ES1 F06
Banksia	Panama	NMNH ES1G06	ES1 G06
carinifera	Namibia	NM L8848	BA18
chrysotoxa	Madagascar	NMNH ES8 G02	ES8 G02
chrysotoxa	Madagascar	NMNH ES8 D02	ES8 D02
cingulifera s.l.	Mozambique	NMNH ES33 A12	ES33 A12
cingulifera s.l.	Mozambique	NMNH ES33 H11	ES33 H11
curialis	New Caledonia	NMNH ES1 A05	ES1 A05
curialis	New Caledonia	NMNH ES1 G04	ES1 G04
curialis	New Caledonia	NMNH ES1 H04	ES1 H04
Curialis	New Caledonia	NMNH ES33 D07	ES33 D07
duplicata	Bangladesh	Allmon, personal	BA2
fortilirata	Japan	NSMT MO 78927	BA14
fuscomaculata	Madagascar	NMNH ES12 B07	ES12 B07
leeuwinensis	Papua New Guinea	NMNH ES33 B02	ES33 B02
madagascariensis	Madagascar	NMNH ES10 D03	ES10 D03
madagascariensis	Mozambique	NMNH ES33 B12	ES33 B12
madagascariensis	Mozambique	NMNH ES33 C12	ES33 C12
madagascariensis	Mozambique	NMNH ES33 D12	ES33 D12
quadrata	Tasman Sea	TMAG E55884	BA28
roseus	New Zealand	NMNH ES5 D03	ES5 D03
sanguinea	Madagascar	NMNH ES12 H06	ES12 H06
sanguinea	Madagascar	NMNH ES12 A09	ES12 A09
sanguinea	Madagascar	NMNH ES22 F09	ES22 F09
terebra	Australia, Northern Territories	MAGNT unregistered	BA36

Table 1.2: Primer pairs for each gene region.

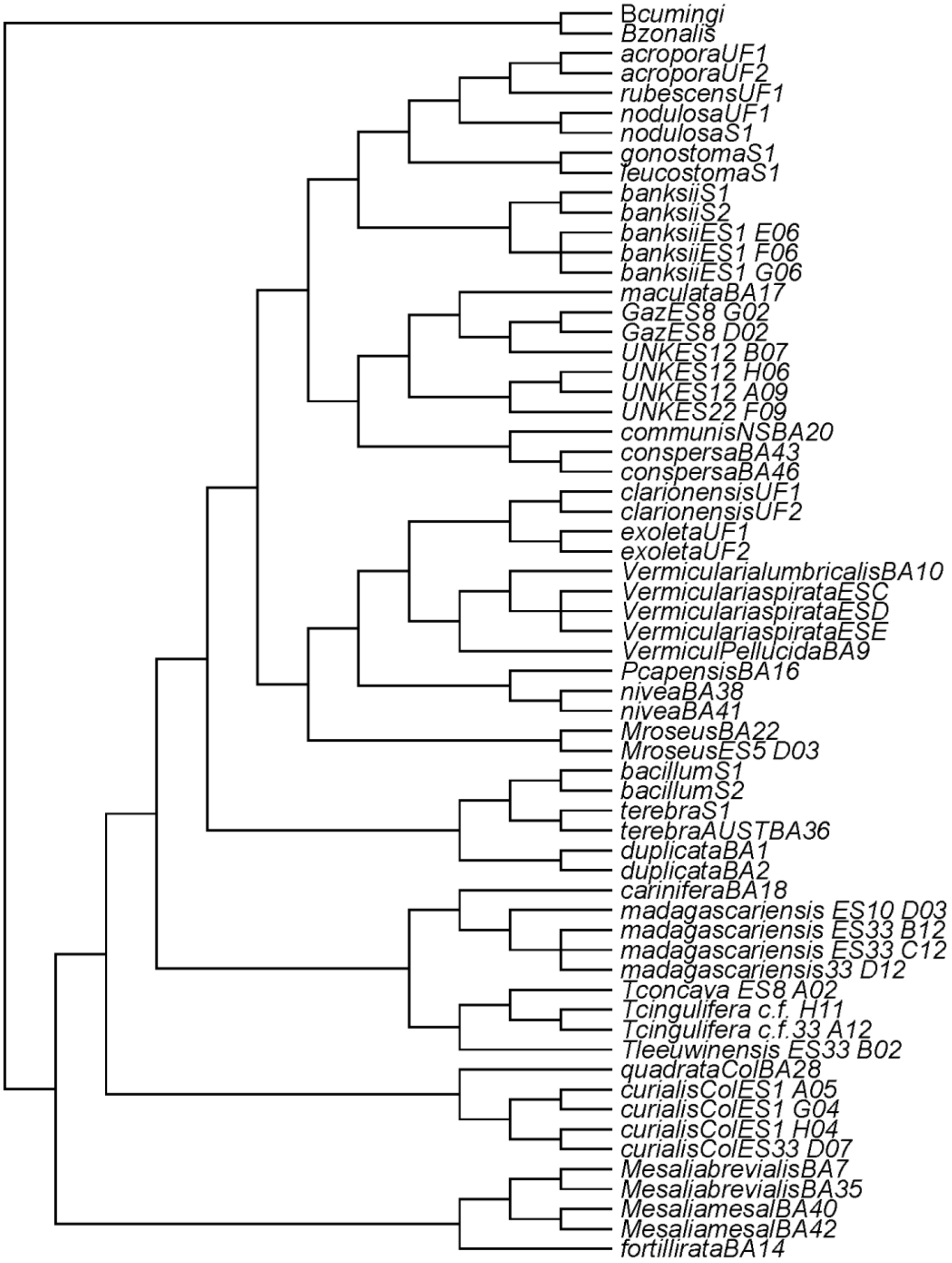
Gene Region	Forward Primer	Reverse Primer	Length
16S	**16Sar:** 5' CGC CTG TTT ATC AAA AAC AT 3' (Simon et al. 1991)	**16Sbr:** 5' CCG GTC TGA ACT CAG ATC ACG T 3' (Simon et al. 1991)	527 bp
12S	**12SF:** 5' AAA GCT TCA AAC TGG GAT TAG ATA CCC CAC TAT 3' (Zou et al. 2011)	**12SR:** 5' TGA CTG CAG AGG GTG ACG GGC GGT GTG T 3' (Zou et al. 2011)	456 bp
H3	**H3NF:** 5' ATG GCT CGT ACC AAG CAG AC 3' (Colgan et al. 1998)	**H3NR:** 5' ATR TCC TTG GGC ATG ATT GTT AC 3' (Colgan et al. 1998)	376 bp

Results

Phylogenies were consistent in broad pattern regardless of method. Maximum parsimony (Figure 1.1), maximum likelihood (both the single best tree, Figure 1.2, and the 70% bootstrap consensus, Figure S1.4), and Bayesian (Figure 1.3) analyses recognized *Neohaustator fortilirata* as sister to a monophyletic *Mesalia* as the most basal turritellid divergence. A monophyletic *Colpospira* was then sister to the remaining species. These contained 2 large clades; One consisting of West Indian Ocean species and *leeuwinensis* and another with *Turritella* s.s. + *duplicata* as sister to all remaining species. All analyses recovered *Colpospira*, *Kurosioia* (Garrard, 1974), *Turritella* s.s., and *Vermicularia*, as monophyletic.

Turritella terebra from southeast Asia and northern Australia exhibited a similar amount of genetic distance to other sister species in the analysis, however only one individual from each region was assessed. Further sampling of *Turritella terebra* from throughout the range attributed to the species would help to determine whether these represent genetically isolated, cryptic species.

Figure 1.1. Strict consensus of 9 maximum parsimony trees constructed in PAUP based on contatenated dataset of 12S, 16S, and H3 and using Batillariidae as a monophyletic outgroup.


Bcumingi
Bzonalis
acroporaUF1
acroporaUF2
rubescensUF1
nodulosaUF1
nodulosaS1
gonostomaS1
leucostomaS1
banksiiS1
banksiiS2
banksiiES1 E06
banksiiES1 F06
banksiiES1 G06
maculataBA17
GazES8 G02
GazES8 D02
UNKES12 B07
UNKES12 H06
UNKES12 A09
UNKES22 F09
communisNSBA20
conspersaBA43
conspersaBA46
clarionensisUF1
clarionensisUF2
exoletaUF1
exoletaUF2
VermicularialumbricalisBA10
VermiculariaspirataESC
VermiculariaspirataESD
VermiculariaspirataESE
VermiculPellucidaBA9
PcapensisBA16
niveaBA38
niveaBA41
MroseusBA22
MroseusES5 D03
bacillumS1
bacillumS2
terebraS1
terebraAUSTBA36
duplicataBA1
duplicataBA2
cariniferaBA18
madagascariensis ES10 D03
madagascariensis ES33 B12
madagascariensis ES33 C12
madagascariensis33 D12
Tconcava ES8 A02
Tcingulifera c.f. H11
Tcingulifera c.f.33 A12
Tleeuwinensis ES33 B02
quadrataColBA28
curialisColES1 A05
curialisColES1 G04
curialisColES1 H04
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MesaliamesalBA42
fortilliratаBA14

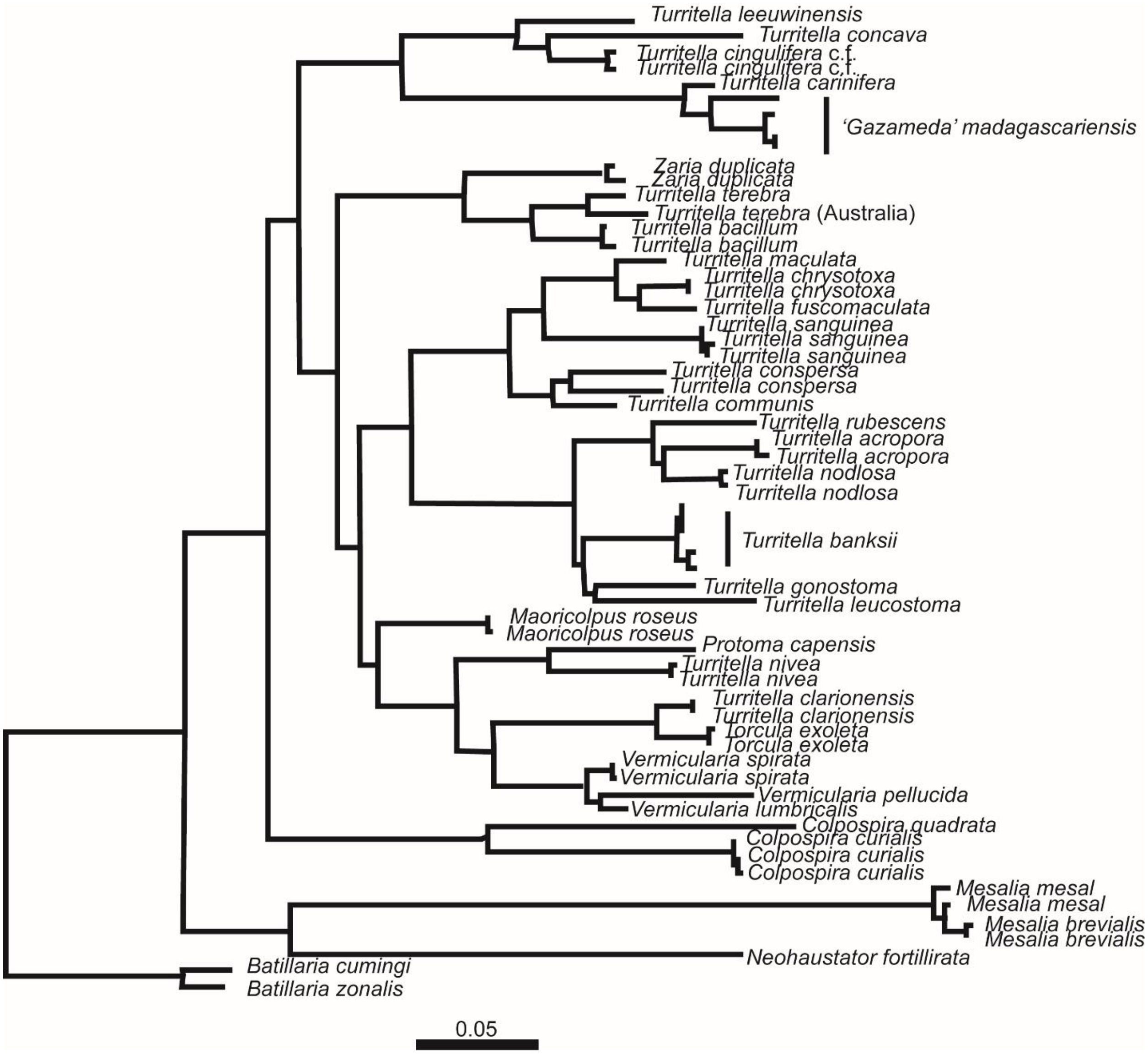

Figure 1.2. Maximum Likelihood reconstruction constructed using RAxML, based on contatenated dataset of 12S, 16S and H3 using Batillariidae as a monophyletic outgroup.

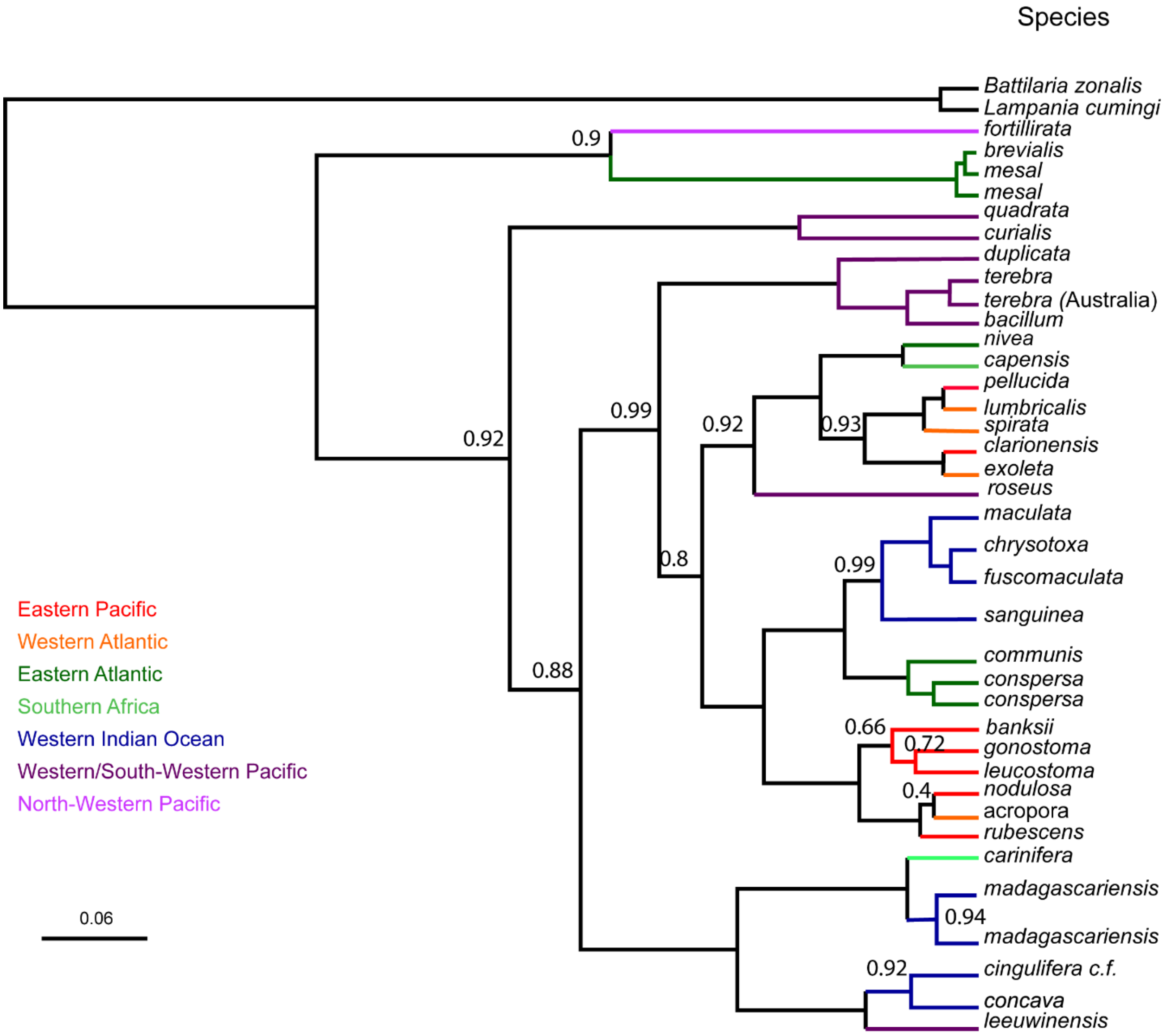

Figure 1.3. Bayesian phylogeny of Turritellidae constructed using BEAST based on H3, 12S, and 16S using Batillariidae as a monophyletic outgroup. Posterior probabilities less than 1 indicated at nodes. Biogeographic regions indicated by colors.

Discussion

Assignment of generic names

At least 35 generic or subgeneric names have been proposed for fossil or extant species belonging to the subfamily Turritellinae (Allmon, 1996), with few coming into general use. Our phylogeny suggests that of previously proposed genera or subgenera with extant representatives sampled in our analysis, *Colpospira*, *Kurosioia* (elevated here from subgenus to genus), *Maoricolpus*, *Mesalia*, *Neohaustator*, *Torcula*, *Turritella* s.s, and *Vermicularia* all represent monophyletic lineages with molecular distances corresponding to divergences from sister taxa at least as old as the Miocene (Figure 1.4). *Protoma* was only represented by a single species, but also appears to meet this criterion. *Zaria*, represented by *duplicata*, is monotypic, and is sister to *Turritella sensu stricto*. Assigning *duplicata* to its own genus does reflect a relatively deep divergence, while assigning it to *Turritella* conveys its sister relationship to *Turritella* s.s. and the significant phylogenetic distance *of Zaria duplicata* + *Turritella terebra* from the remaining Turritellinae. We propose retaining *duplicata* in the genus *Turritella*, as this arrangement conveys the most information about evolutionary relationships among Turritellid genera, and minimizes the number of genera in use.

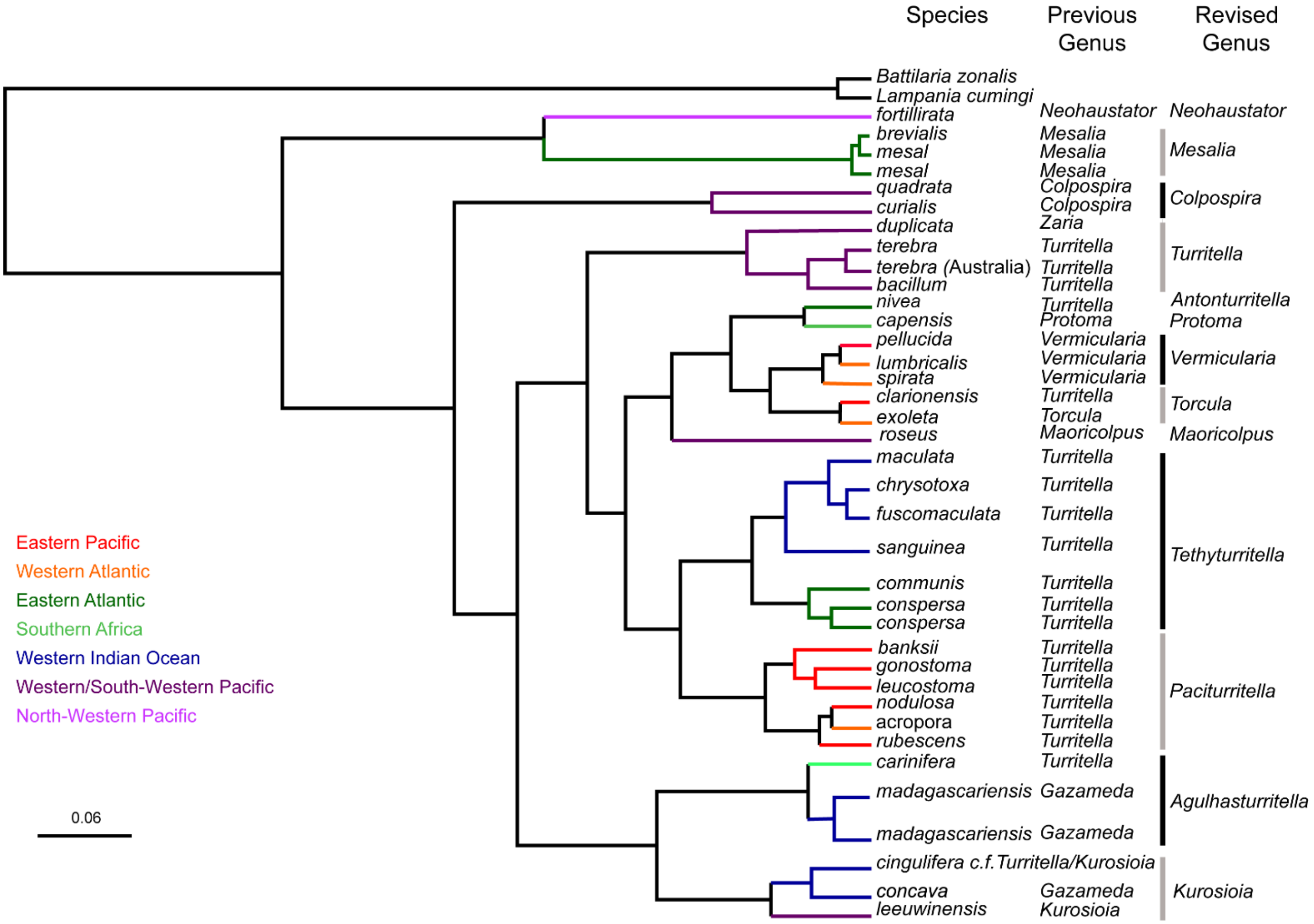

Figure 1.4. Proposed generic revision of Turritellidae mapped on the Bayesian phylogeny (figure 1.3).

As all of these generic names predate molecular analysis of the group, they have already been defined based on unique morphological characters or character combinations. *Colpospira* is identifiable based on an exceptionally deep and narrow lateral sinus, and typically possesses a quadrate aperture (Garrard, 1972). *Kurosioia* is identified by primary spiral sculpture appearing in the order C-B-A, with C beginning as a strong keel and later resembling other ribs, well developed lateral and basal sinuses, weak inflection of the lateral sinus, and a C cord which does not shift abapically

(Garrard, 1972; 1974; Ida, 1952; Marwick, 1957a). *Maoricolpus* possesses a conic, multispiral, styliform protoconch, with spiral cords appearing in the order B,C, A, with B as the dominant cord on the earliest teleoconch before it subsides (Garrard, 1972; Marwick, 1957a). *Mesalia* is identifiable based on the presence of a slight basal spout and a spiral ridge on the columella (Cataldo & Lazo, 2016; Marwick, 1957a). *Neohaustator* has an adapically located lateral sinus, with a double arch, and primary spiral cords which appear in the order C-B-A (Ida, 1952; Marwick, 1957a). *Torcula* possesses a well-developed lateral sinus, quadrate aperture, and typically has beaded spiral sculpture dominated by two strong cords. *Protoma* has spiral sculpture which appears in the order C-B-A with B following several whorls after C*,* and a unique notch in the basal sinus(Marwick, 1957a). *Turritella* s.s. has primary spirals appearing in the order B-A-C, with a secondary spiral between A and B forming before C (Marwick, 1957a). If *Zaria* is retained, it is identifiable based on similarity to *Turritella* s.s., but distinguishable from *Turritella* s.s. by retaining the spiral sculpture onset pattern C-B-A. *Turritella* + *Zaria* are recognizable as a clade by the extremely prosocline lateral sinus trace (Marwick, 1957a). *Vermicularia* is identifiable through its uncoiled morphology (Anderson et al. 2018). *Gazameda,* which was unavailable for additional sequencing, is also likely to be a reliable group, native to Australia, when only taxa possessing an enlarged, scaphelloid protoconch (Garrard, 1972; Marwick, 1957a).

Retention of genera recognizable based on morphological criteria, and representing lineages which have been divergent since at least the Miocene necessitates the erection of additional genera based on considerations of monophyly. Most of these clades are biogeographically restricted, and we therefore propose generic names reflective of this fact. We are confident in the stability of these clades as Bayesian analysis resulted in posterior probabilities of 1 for the base of each clade and ML bootstrap values were 0.9 or better. We propose *Aghuilhausturritella* for the clade of *carinifera* + *madagascariensis*, after the Aguilhaus Current running South between Madagascar and East Africa, with *Gazameda madagascariensis* as the type species, *Tethyturritella* for the clade of *communis* + *maculata,* representing a clade that appears to have originated before the closure of the Tethys connection between the Indian and Atlantic Oceans, with *maculata* as the type species, and *Paciturritella* for the clade of *nodulosa* + *gonostoma* representing most modern East Pacific turritellids and the geminate species acropora (Sang et al., in review), with *leucostoma* as the type species. Recognition of *Protoma* also requires new generic assignment for *Turritella nivea* which lacks the diagnostic deep lateral sinus of *Protoma*. We propose *Antonturritella* for Hermann Eduard Anton, who originally described *Turritella nivea*.

Biogeography

Broad biogeographic provinces were defined as Eastern Pacific, Western Atlantic, Eastern Atlantic, Southern African (South Africa), Western Indian Ocean (Red Sea to Mozambique and Madagascar), Northwest Pacific (Japan), and Western/Southwest Pacific (Bangladesh to Australia and New Zealand). Long distance dispersal of turritellids has long thought to be rare, due to their short (or absent) planktonic larval stage (Allmon, 2011; Sang et al., in review). This appears to be correct as most clades are remarkably consistent in biogeography with *Maoricolpus* being a notable exception. While most clades appear to consist of species from the same or neighboring biogeographic provinces,

Conclusions

Now that a framework molecular taxonomy exists for turritellids we may begin to organize their taxonomy in a way that permits understanding of their evolutionary history. Subfamilies of Turritellidae should be reorganized to reflect monophyletic groups. Bouchet et al. (2005) recognized 5 subfamilies; Orectospirinae Habe 1955, Pareorinae Finlay and Marwick 1937, Protominae Marwick 1957, Turritellinae Loven 1847, and Vermiculariinae Das 1913. We did not include Orectospirinae in the analysis. Turritellinae is paraphyletic with respect to Vermiculariinae, Protominae, and "*Zaria*" *duplicata* (which had been placed in Pareorinae by Marwick (1957). We therefore propose a new system reflecting the deepest divergences in the phylogeny – Pareorinae including *Mesalia* and other spout-bearing taxa (Cataldo & Lazo, 2016; Squires & Saul, 2007), Neohaustatorinae (*Neohaustator*), and Turritellinae encompassing all other taxa in our analysis (including *Vermicularia*, *Maoricolpus*, *Kurosioia, "Zaria" duplicata, Protoma, Torcula, Turritella* s.s.).

From the perspective of conchological or paleontological studies, this molecular phylogeny presents mixed results. Unlike the traditional morphology based taxonomy of corals (Budd et al., 2010; Fukami et al., 2004), many traditionally recognized groups (genera) of turritellids have proven to be reliable, monophyletic and deeply divergent lineages. In contrast to Conidae, which has diversified rapidly and relatively recently (Puillandre et al., 2014a), our molecular results suggest several clades exist which are biogeographically restricted and represent lineages of substantial age. Many of these have been previously recognized based on unusual morphological characters or combinations of characters, particularly characters related to protoconch morphology or onset of spiral sculpture (Allmon, 1996; Finlay & Marwick, 1937; Finlay, 1926; Ida, 1952; Kotaka, 1959; Marwick, 1957a), but also unusual lateral or basal growth line forms (Fig. S1.3; (Allmon, 1996; Cossmann, 1912; Marwick, 1957a). This suggests that taxa retaining plesiomorphic morphologies are difficult to place in phylogenetic context, but identifiable lineages have proven reliable (*Mesalia*, *Colpospira*, *Turritella* s.s., *Protoma*, *Vermicularia*, *Maoricolpus,* and *Kurosioia*). Future examination of protoconch morphology and pattern of spiral sculpture onset will hopefully provide shell-based characters for the recognition of *Antonturritella*, *Tethyturritella*, *Paciturritella*, and *Aghulasturritella.* We suggest continuing the common practice (Allmon, 1996; Hendricks et al., 2014; Ryall & Vos, 2010) of assigning species to "*Turritella sensu lato*" if they do not share synapomorphies for any named genus, but with the explicit recognition that this is not a monophyletic group, as the genera recognized or established here are supported to be.

The operational practice of considering fossils or conchologicaly defined species in basins/biogeographical provinces to most frequently be related to other species in the same basin/province appears to be generally, but not universally, reliable. For example, the fossil Turritellids of the American Neotropics are likely classifiable as *Torcula*, *Vermicularia*, or *Paciturritella*, but in practice a plesiomorphic species early in the evolution of *Torcula* or *Vermicularia* would likely be assigned to *Paciturritella*, unless sufficient synapomorphies can be defined for *Paciturritella*. Documenting the protoconch and earliest teleoconch whorls of as many fossil and Recent species in the biogeographic region as possible is the logical next step in a strategy to identify shell characters useful for assigning species to supraspecific taxa.

The molecular phylogeny has resolved several outstanding questions in turritellid taxonomy:

1. The hypothesis that turritellids only rarely undergo long-range dispersal events is affirmed.
2. Several clades which have previously been recognized at the generic level based on protoconch morphology, order of appearance of spiral sculpture, or unusual growth line morphology, are supported as deeply divergent monophyletic lineages.
3. Four additional genera are proposed which require systematic analysis of protoconch morphologies and onset of spiral sculpture in order to determine potential morphological synapomorphies.
4. The close relationship between *Neohaustator* and *Mesalia* is unexpected, however *Mesalia* diverged from Turritellinae at least by the Cretaceous, and *Mesalia* was formerly wide-ranging (Cataldo & Lazo, 2016; Squires & Saul, 2007).
5. The phylogeny affirms the hypothesis that similar adult spiral sculpture patterns and whorl profiles have originated through parallelism in different basins.

Acknowledgements

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Chapter 2: Systematics and Evolution of fossil and Recent *Vermicularia* (Gastropoda: Turritellidae)

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Abstract— *Vermicularia* (Cerithioidea: Turritellidae) are a clade of Miocene-Recent gastropods with an unusual uncoiled shell morphology. Like other 'worm-snails', they are systematically troublesome, and although earlier work affirmed the turritellid affinity of one species, monophyly, systematic relationships to other turritellids, and systematic relationships within the clade have not been previously examined. Here we present a molecular taxonomy of turritellids, including members of the proposed genera *Mesalia, Zaria, Torcula, Protomella, Maoricolpus*, in order to establish the monophyly of *Vermicularia* determine higher level relationships. We provide a revised taxonomy with more detailed diagnoses for all known living and fossil species, including the synonymy of *V. lumbricalis* Linneaus and the commonly used junior synonym *V. knorrii* Deshayes. The new early Pliocene species *Vermicularia katiae* is described from the Dominican Republic. The phylogenetic relationships within living and fossil Vermicularia are also established based on morphological characters and with close out-group turritelliform species chosen based on the molecular phylogeny. The reconstructed phylogeny indicates that new species arose via cladogenesis much more frequently than by anagenesis, with most lineages originating in the Pliocene, but prior to the complete closure of the Central American Seaway.

INTRODUCTION

The need for more accurate and thorough systematics, especially for invertebrates has been noted by many authors (Agnarsson and Kuntner, 2007; Allmon, 2011; Bouchet and Strong, 2010; Feldmann and Manning, 1992; Regnier et al., 2009; Savage, 1995; Wilson, 2004; Winston, 1992). Vermiculariinae (Dall, 1913) is a Miocene-Recent clade of turritelline gastropods consisting of the genera *Vermicularia*, Lamark, 1799, and *Callostracum*, Smith, 1909 (MolluscaBase, 2018) which share an openly coiled morphology (Figures 2.1 and 2.2). Here we follow Yochelson (1971) in distinguishing open coiling (in which whorls are not in contact with previous whorls but may maintain the same coiling axis) from uncoiling (in which the coiling axis itself becomes irregular). *Vermicularia* are of ecological interest, as they can be important or even primary components of bioherms (biogenic reefs; Figure 2.3) e.g.(Pearse and Williams, 1951). They are also of evolutionary interest as, compared with other uncoiled gastropods, *Vermicularia* are relatively recently evolved (Miocene), and remain the most similar to their regularly coiled turritellid relatives (Morton, 1953; 1955; Bieler and Petit, 2014). They are also the only group in which regular coiling appears to have been re-evolved in a population (Gould, 1969; Gould and Robinson, 1994), and the uncoiled portion of the shell also appears to have been secondarily reduced in *V. fargoi owensi* (Petuch and Myers, 2014).

The goals of this systematic review are threefold: to determine appropriate taxonomic nomenclature for the Vermiculariinae, to determine the phylogenetic history of the group, and to clarify for researchers and collections managers the characters used to properly identify species of this troublesome genus. This last is a non-trivial point, as collections data are increasingly available for analyses through systems such as the paleobiology database (www.paleodb.org), rampant misidentifications can affect analyses of biodiversity and biogeography. To that end, all biogeographic information presented herein has been confirmed with specimen data (in collections; see table 2.1; or figured in publications) by us, or the authors who named the species in question, and so represents a conservative estimate of species stratigraphic and geographic ranges.

“Worm-snails”, the polyphyletic term applied to uncoiled or openly coiled gastropods with an elongated (*i.e.* vermiform) morphology, belonging to the families Vermetidae, Siliquariidae, and the genus *Vermicularia* within Turritellidae, are a particularly problematic group in gastropod systematics (Bieler, 1993). Vermiform gastropods have been the subject of extensive taxonomic confusion (e.g., Gould and Robinson, 1994, referred to vermetid taxonomy as “a nightmare”). Taxonomic issues have occurred at all levels including the initial assumption that all uncoiled or openly coiled gastropods were a single taxonomic group, confusion of nominal gastropod and polychaete taxa, and the naming of species and subspecies based on ecophenotypic characteristics of uncoiling (Keen, 1961; Bieler and Petit, 2011; Golding et al., 2014). While previous research has made progress in determining the validity and proper assignment of named vermiform species (Morton, 1953; Bieler and Hadfield, 1990; Lieberman, 1993; Bieler, 2011), this paper redescribes and provides synonymies for species in this group, and is also the first to demonstrate the relationship of Vermiculariinae to other turritellid gastropods using a molecular phylogeny with more than one *Vermicularia* species, as well as the first to provide a morphological phylogeny of valid Recent (Figure 2.1) and fossil (Figure 2.2) species.

Misidentifications of *Vermicularia* species appear to typically occur by assigning all specimens to the most common species from the region or geologic formation. This has been exacerbated by a history of naming *Vermicularia* species without properly examining specimens, especially the types, of other named species, or with apparent reference to misidentified examples of the previously named species. There is substantial overlap in the use of common names, with the name “West Indian Wormsnail” applied variably to any of multiple Recent species, and the common name “Florida wormsnail” used to refer either to *Vermicularia fargoi* or *V. knorrii* depending on the author (e.g., Witherington and Witherington, 2017; Rehder et al., 1991). Further confusion has resulted from the mislabeling of locality information for *Vermicularia lumbricalis* as “habitat in indiis” (Linnaeus, 1758), while all known species belonging to the *Vermicularia* are Atlantic or Eastern Pacific.

Vermicularia can be distinguished from the other worm-snails readily if the soft tissues or early teleoconch are present. Siliquariidae are distinguished from *Vermicularia* by their lack of pallial tentacles, inflated teleoconch, deep slit that may be closed off periodically producing perforations, whorls with minimal contact with one another, and hairy opercula (Morton, 1955; Rehder, 1981; Bieler, 1996; Healy and Wells, 1998; (Tunnell et al., 2010). Vermetids typically have very small coiled larval shells, but subsequently may grow in straight tubes or a truly irregular fashion. Vermetids, like *Vermicularia,* may also form large bioherms with conspecifics or other colonial organisms (Petuch and Myers, 2014; Witherington and Witherington, 2017). *Vermicularia,* however, always have early teleoconch sections which are regularly (tightly) coiled, resembling turritellids in all respects prior to uncoiling, and have apertures of similar shapes to other turritellids even after uncoiling (e.g., not always round, sometimes quadrate, subquadrate, teardrop shaped). A tightly coiled early teleoconch, coupled with strong spiral, but not axial sculpture on the whorls is highly suggestive of turritellid affinity, as opposed to other vermiform snails.

Vermicularia also do not completely lack coiling direction, most typically adopting a new coiling axis as they cement to a substrate and maintaining that axis until further changes are dictated by the substrate (the plasticity to change the direction of the aperture as needed while generally maintaining the same spiral coiling direction). The orientation of the aperture upwards in most species removes them from Raup (1966) space, making descriptions in Raup's terminology analogous at best (e.g., if the aperture is now parallel to the former coiling axis, D is infinite and T becomes nearly equal to growth and/or growth time).

Positive assignment of fossil molds is extremely difficult, although the presence of axial ridges (perpendicular to growth direction), as opposed to spiral sculpture, would appear to exclude the *Vermicularia*. *Vermicularia* shells may show signs of cementation scars, although these are often weak. Where they co-occur, fossil *Vermicularia* tubes, in the absence of apices, may be distinguished from worm tubes by;

1. Generally larger diameter of gastropod shells
2. Distinct or subtle coiling that generally maintains the same axis
3. The presence of turritellid spiral sculpture or growth lines,
4. Consistent crossed-lamellar aragonitic shell microstructure (polychate tubes appear to exhibit a much wider variety of microstructures, including fine

complex crossed lamellar, spherulitic prismatic, simple prismatic, ordered chevron, or irregular microstructures)

5. Internal dome shaped septa occur in gastropod rather than polychaete material (Anderson and Allmon, 2018; Vinn, 2005, 2013; Vinn et al., 2008).
6. Turritellid shells are exclusively aragonitic originally, while polychaete tubes are typically bimineralic, with one polymorph dominant (Vinn et al., 2008).

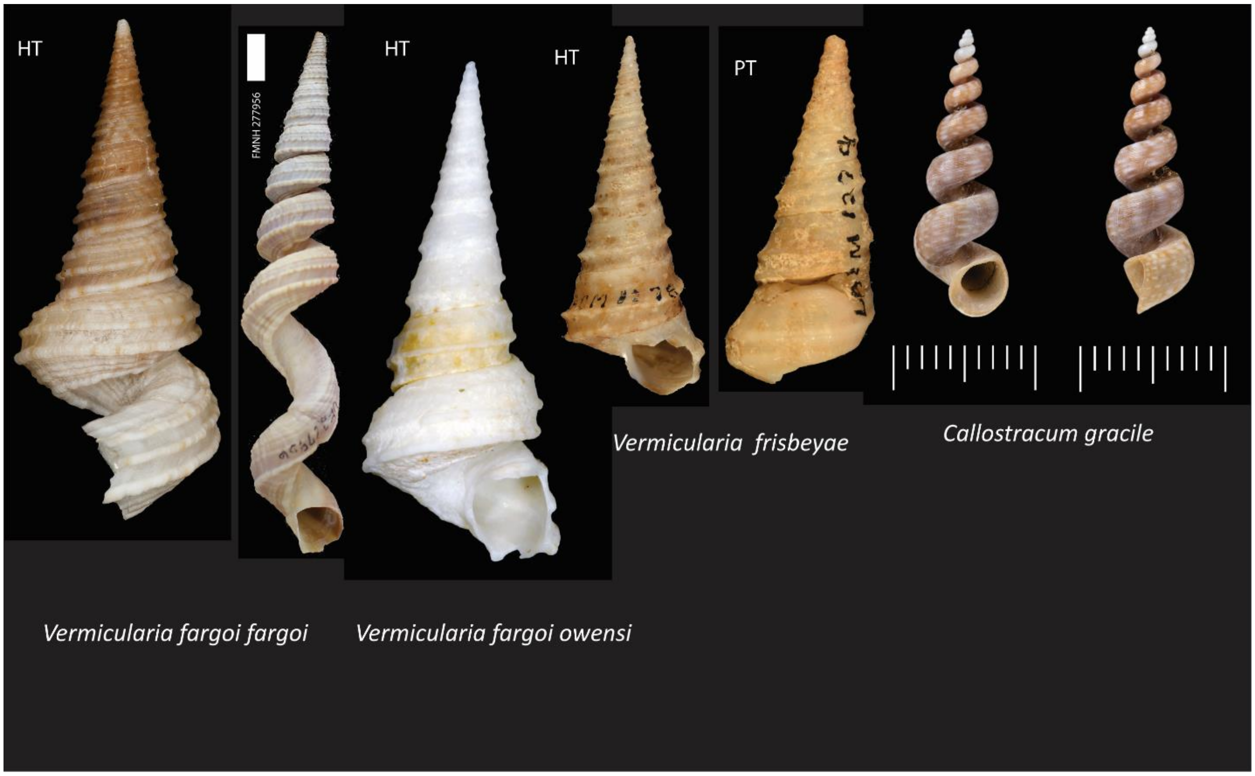


Figure 2.1. Extant species of *Vermicularia* and *Callostracum*. Scale bars 1 cm unless otherwise indicated. Holotype indicated by “HT”, paratype by “PT”, Neotype by “NT”, and an illustration of lost type material used as epitype (informal) for *V. knorrii* designated with “ET”.

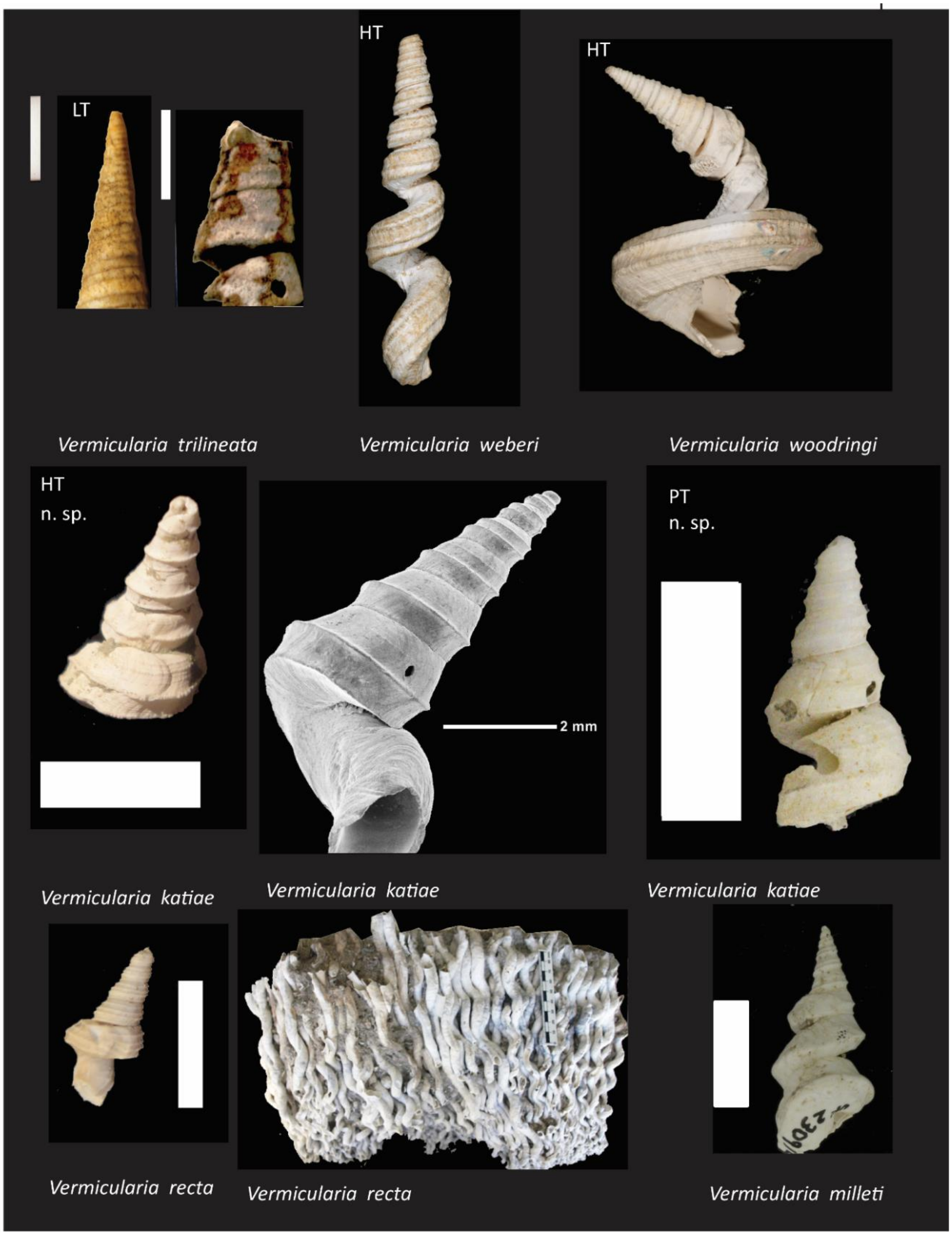


Figure 2.2. Fossil species of *Vermicularia*. Scale bars 1 cm, except for *V. recta* reef where each black or white bar is 1 cm. Holotype designated by “HT”, Paratype by “PT”, lectotype by “LT”.

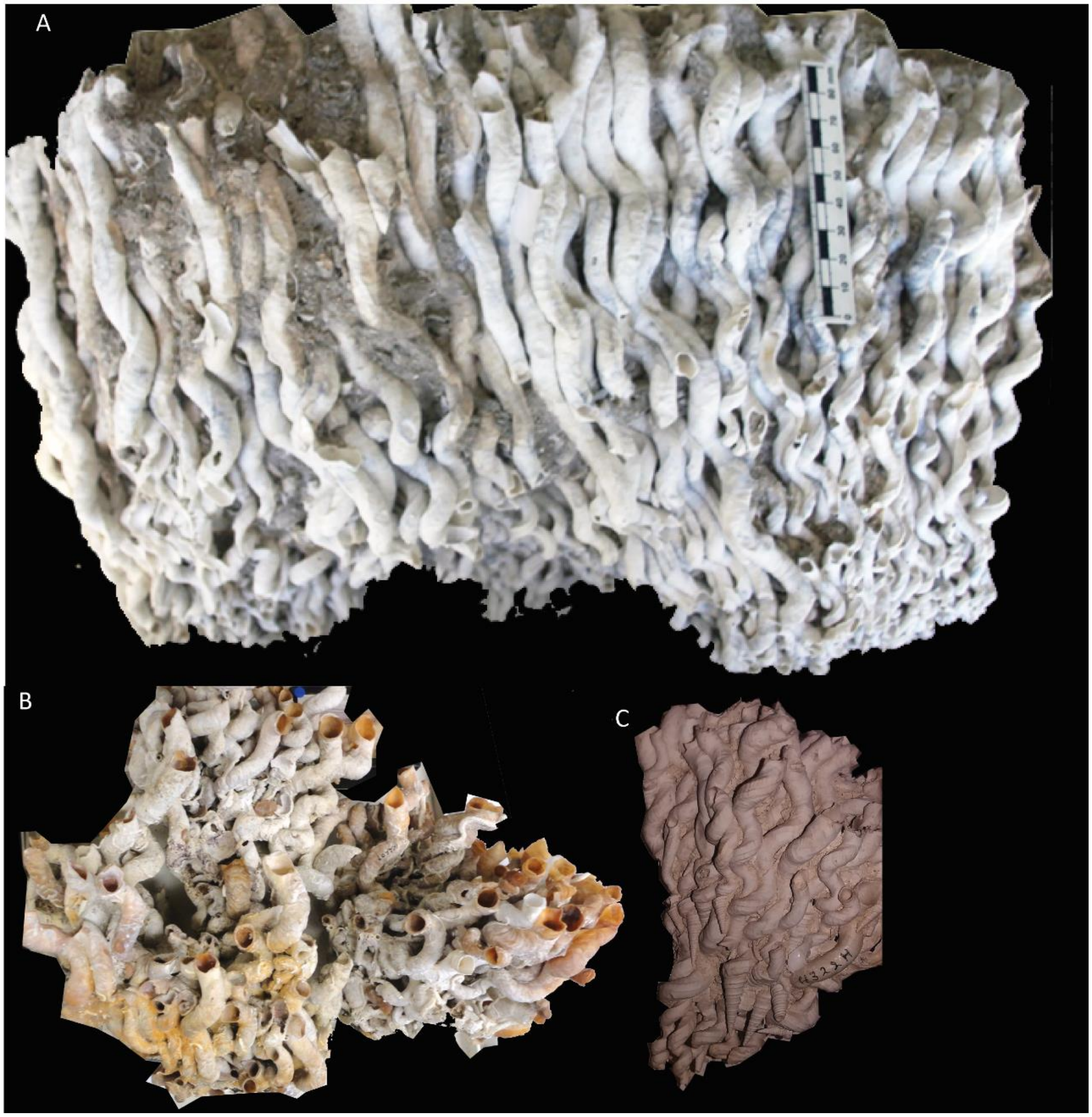


Figure 2.3. *Vermicularia* species known to form reef structures. A. *V. recta* B. *V. spirata* C. *V. woodringi*

Natural History

Habitat and Ecology

Living *Vermicularia* may be significant or numerically dominant components of their local molluscan communities (Barrientos-Lujan et al., 2017; Gould, 1968).

Vermicularia are typically attached to a hard substrate, such as coral, rocks, or conspecifics, but can be found living within sponges as well (Gould and Robinson, 1994; Bandel and Kowalke, 1997; (Barrientos-Lujan et al., 2017; Sept, 2016; Tunnell et al., 2014)). *V. fargoi* are an exception, being typically found unattached on sand or mud (Olsson, 1951; Petuch and Myers, 2014). Uncoiling results in limited mobility, but permits rapid upward growth towards food sources and growth around obstacles (Gould, 1969). Uncoiling is typically expected to result in increased susceptibility to predation (Yochelson, 1971), based on applying torque to the shell or attacking the aperture; however, the cemented habit, often within corals or sponges, or formation of bioherms with conspecifics mitigates this pressure, providing refuge from both predation and physical disturbance (Barrientos-Lujan et al., 2017; Gibson et al., 2011; Kelaher et al., 2001). Uncoiling appears to be ecophenotypic in some species of Vermiculariinae, with *Vermicularia spirata* uncoiling earliest in ontogeny in the presence of their preferred host, the branching coral *Oculina*, later, on substrates such as massive corals, and only rarely in the coral free environment of Walsingham Pond, Bermuda (Gould, 1969; Gould and Robinson, 1994). Other species, such as *V. fargoi*, uncoil without any attachment. Nevertheless, typical uncoiling widths (mid-whorl diameter of the last whorl prior to the loss of contact between whorls, *i.e.* the last whorl in complete contact with the previous whorl) or whorl numbers may help to discriminate species, so long as these are not the sole criteria employed.

Most species of *Vermicularia* inhabit shallow subtidal environments, with *V. bathyalis* being a notable exception (Oleinik et al., 2012; Petuch, 2002; Sept, 2016). The deepest dwelling species are *V. bathyalis* Petuch and *V. lumbricalis* (*knorrii*), recorded at ~600 and ~500 m on the Texas continental slope (Oleinik et al., 2012; Tunnell et al., 1978, 2010), respectively. As *V. bathyalis* is most similar to *V. knorrii* among all other *Vermicularia* species, and has a broader depth range, it is possible that reports of *V. knorrii* in Texas may be examples of *V. bathyalis*, greatly expanding the range of this species. Unfortunately, we have not been able to examine any deep-water Texas specimens. Synonymy may also be unlikely as *V. bathyalis* appears to be highly endemic and is likely isolated by the powerful currents in the Straights of Florida, but the constriction, deflection, and merger of currents in the Straights of Florida also provides downwelling of warm surface waters and plankton (Oleinik et al., 2012). Strong (up to 50 cm s^{-1}) bottom currents provide *V. bathyalis* with an unusual hardground environment, with a moving veneer of soft sediments (Oleinik et al., 2012). Temperatures are observed to be around 16.5° C at 400 m, in contrast, temperatures of 7.5°C are present on the Florida side of the Straights at similar depths (Malloy and Hurley, 1970; Oleinik et al., 2012; Sverdrup et al., 1942). Most species, including *V. bathyalis*, are associated with reef habitats or other hardgrounds, however *V. fargoi* is found in sandy lagoons and muddy habitats (Petuch and Myers, 2014). Several species of *Vermicularia* (*recta, spirata,* and *woodringi*) are known to inter-coil with other conspecifics, only lightly cemented together, but physically wrapped around one another, forming bioherms that can weigh several kilograms and even be of stratigraphic significance (Phillipi, 1836; Hyatt Verrill, 1936; Olsson and Harbison, 1953; (Allmon, 1992c).

Soft Part morphology

Vermicularia spirata soft tissues have been described by Hughes (1985), Healy and Wells (1998), Bieler and Hadfield (1990), and Stimpson (1851), Stimpson referring to the species as *Vermetus radicula*. Soft anatomy resembles other turritellids (Morton, 1953, 1955; Allmon 2011), with an elongated mantle cavity and the apical part of the visceral mass occupied with digestive glands and reproductive organs. The foot resembles other turritellids and remains functional in *Vermicularia*, even if they spend most of their lives in place, cemented, the adults can and do move (Gould, 1969; Hughes, 1985, Allmon, 2011; contra Morton, 1953;). Although they may retain the ability to move into adulthood, Bandel and Kowalke (1997) report that after attachment the foot becomes reduced and functions primarily to manipulate the operculum. The operculum is corneous, concentric, black, and hard at the center and surrounded by a thin, membranous, flexible portion, about one fourth its diameter (Stimpson, 1851), and lacks bristles (Morton, 1953). This flexible portion allows the animal to seal the aperture with the operculum, but also permits further retreat into the shell (Stimpson, 1851).

Vermicularia retain small pallial tentacles (papillae) similar to other turritellids (Tunnell et al., 2010). In most turritellids (which live semi-infaunally) these serve to prevent sand, mud, or other debris from entering the mantle during feeding. *Vermicularia*, like other turritellids are ciliary filter feeders, and have an expanded mantle cavity which elongates the gill surface employed in feeding (Andrews, 1974; Peel 1975; Allmon, 2011). They possess tentacles at the mantle edge (pallial tentacles), which in semi-infaunal turritellids help to keep debris from entering the mantle (Hughes, 1985; Healy and Wells, 1998; Allmon 2011).

Reproduction

The reproductive biology of *Vermicularia spirata* was thoroughly treated in Bieler and Hadfield (1990). *V. spirata* is a protandrous hermaphrodite, in which juvenile males are free-living, and become attached and uncoiled when they undergo sex change. The paraspermatozoa of *V. spirata* are multiflagellate (Bieler and Hadfield, 1990). Stimpson (1851) noted that eggs of *V. radicula* (*spirata*) near Buzzard's Bay, Massachusetts, were deposited in July, in a mass shaped like an elongated cone bent into a half circle. Like other turritellids they are susceptible to castration by trematode parasites (Perez, 1936) with Bieler and Hadfield (1990) reporting 17% of *V. spirata* examined infested.

Current Status of Taxonomy

Previous molecular analysis by Lieberman et al. (1993) confirmed *Vermicularia knorrii* as a member of Turritellidae, as had long been suspected based on morphology (Morton, 1955), nested among species usually assigned to *Turritella*. Here we expand on this finding by incorporating evidence from multiple genes and multiple *Vermicularia* species with new data from Tropical Eastern Pacific and Atlantic turritellids to establish monophyly of the group and determine their closest relatives. We also have analyzed morphological characters for all valid Recent and fossil species within the Vermiculariinae to construct a phylogenetic tree documenting the clade's history.

A large number of species have been named in the genus *Vermicularia* or Vermiculariinae in error, and we have provided a reference table of these names in the supplementary information (S2.1; see also Bieler, 1993). Of particular relevance to the evolutionary history of the group are the taxa *Laxispira* and '*Pseudomesalia'* (Douvillé, 1916). Vermiculariinae is occasionally reported as originating in the Cretaceous, based on missasignment of the uncoiled genus *Laxispira* Gabb 1877 to the Vermiculariinae;

however, this genus does not belong to Turritellidae, and should be assigned either to Vermetidae (Bandel and Kowalke, 1997) or as a slit-less siliquariid (Bieler and Petit, 2011). '*Pseudomesalia'* is a preoccupided by the Coleoptera (Ganglbauer, 1900), but no new name is presently in use for the gastropods assigned to this genus. The group has been mentioned as a relative of either *Vermicularia* or Vermetidae (Cossman, 1925), but is more recently assigned to the Cassiopidae (Kollmann, 1979, Pereira et al., 2016). Pereira et al. (2016) find that '*Pseudomesalia'* possesses all the diagnostic criteria of Cassiopidae, which would remove them from consideration as stem *Vermicularia* (an affinity proposed for '*Pseudomesalia'* due to the presence of an umbilicus).

Personal examination of material which was not available online proved vital to this study as a large number of specimens in many collections are misidentified. Common errors include fossil species miss-assigned to the Recent species *Vermicularia spirata*, lots containing multiple species, and confusion among *V. fargoi, V. knorrii*, and *V. spirata* (possibly owing to the application of the common name "Florida wormsnail" to all three species).

Several type specimens appear to have been lost or destroyed. *V. knorrii* Deshayes was named based on Knorr's figure in the Vergnuegen (1757; pl. 17, figure 2) from the Sommer collection, the fate of which is unresolved. We do not here designate a neotype for *V. knorrii* as we conclude it is a junior synonym of *V. lumbricalis*. *V. radicula* Stimpson was destroyed in the 1871 Chicago fire, along with Stimpson's Smithsonian specimens of American invertebrates, his private collection, and all of his manuscripts in preparation. The type of *V. pellucida* Broderip & Sowerby is apparently no longer in the collections of the Natural History Museum, London.*Smithia gracilis*

Maltzan was not found with the Maltzan collection which is now divided between the Natural History Museums of London and Wales). The original specimen of *gracile* accessioned by Smith leading to the erection of the genus *Callostracum* was located, NHMUK 1909.7.27.1, and used as the exemplar of this species. We very strongly support efforts to record the fate of important collections such as these so that taxonomic and evolutionary research can proceed more efficiently (e.g., geocurator.org; Bouchet and Strong, 2010; Taylor, 2016).

MATERIALS AND METHODS

Species and subspecies examined for this study are the Recent species *Callostracum gracile* Maltzan, 1883; *Vermicularia bathyalis* Petuch, 2002; *V. fargoi fargoi* Olsson, 1951; *V. fargoi owensi* Petuch and Myers, 2014; *V. fewkesi* Yates, 1890; *V. frisbeyae* McLean, 1970, *V. lumbricalis* Linnaeus, 1758, *V. knorrii* Deshayes, 1843, *V. pellucida* Broderip and Sowerby, 1829; *V. radicula* Stimpson, 1851; *V. spirata* Phillipi, 1836; the Miocene species *V. milleti* Deshayes, 1839; and the Plio-Pleistocene species *V. katiae*, n.s., *V. recta* Olsson and Harbisson 1953; *V. trilineata* Guppy 1864; *V. weberi* Olsson and Harbisson 1953; and *V. woodringi* Olsson and Harbisson, 1953. Several additional species have been assigned to the genus *Vermicularia* in error and are listed in table S2.1. Institutional abbreviations used are in Table 2.1.

Table 2.1 Institutional abbreviations used.

Abbreviation	**Institution**
ANSP	Academy of Natural Sciences of Drexel University, Philadelphia, Pennsylvania, USA
ES	ES Personal Collection
LACM	Natural History Museum of Los Angeles County, Los Angeles, California, USA
MNHN	Muséum National d'Histoire Naturelle, Paris, France
NHMUK	Natural History Museum, London, UK
PRI	Paleontological Research Institution, Ithaca, New York, USA
UF	Florida Museum of Natural History, University of Florida, Gainesville, Florida, USA
USNM	National Museum of Natural History, Smithsonian Institution, Washington, DC, USA
UUZM	Uppsala University Zoological Museum, Uppsala, Sweden

A significant effort was made to locate live specimens of the unusual population of *V. spirata* from Walsingham Pond, Bermuda, described by Gould (1968, 1969), in which it was observed that the majority of individuals maintain regular coiling throughout ontogeny. Walsingham Pond is a relatively small anchihaline pond in Bermuda, where 2 days of surveying and hand dredging in 2016 by BMA and a field assistant resulted in thousands of dead shells of *V. spirata* being examined, but no live individuals being found at this location. As a previous survey conducted in 1991 of the biotas of Bermudan anchialine ponds (Thomas et al., 1991) also noted the absence of live *V. spirata*, it is likely that this unusual population has been extirpated. Gould (1968) described approximately 95-99% of specimens as retaining coiled morphology at the largest attained sizes, consistent with our own observations of dredged material.

Molecular Methods

Molecular analyses were based on the western Atlantic and tropical eastern Pacific turritellid phylogeny of Sang et al. (in review), with additional sequence data obtained for eastern Atlantic species and species from other putative turritellid genera (*Maoricolpus, Mesalia, Protomella, Zaria*) (Table S2.2). *Batillaria zonalis* and *Lampania cumingi* (Batillariidae) were chosen as the outgroup based on their close relationship to Turritellidae in combined morphological and molecular analysis of Strong et al. (2011; Figure 8). No material amenable to sequencing could be located for the Recent vermiculariine species *V. fargoi* or *C. gracile*.

DNA was extracted using a Qiagen DNeasy kit, following the manufacturer's protocol. The mitochondrial 12S (456 bp), 16S (527 bp), and nuclear H3 (376 bp) regions were chosen as gastropod specific primers were available for these genes (Colgan et al., 1998; Simon et al., 1991; Zou et al. 2011). The PCR protocols used in Sang et al. (in review) were followed for additional species, including 0.002 μg/μL bovine serum albumen to improve PCR yields (Woide et al., 2010; Farell and Alexandre, 2012). Sanger sequencing was performed at the Cornell University Biotechnology Resource Center. Sequence data was added to the alignment of Sang et al. (in review), aligned with MUSCLE (Edgar, 2004), and visually checked using Mesquite v 3.40 (Maddison and Maddison, 2018).

Morphological characters

Turritellids are generally acknowledged to have a paucity of shell characters, despite having moderately high modern (~150 species) and fossil (~ 800 species) diversity ("prodigious taxonomic diversity but relatively little morphological disparity"; Allmon, 1996, 2011). By combining morphological analysis with outgroup choices derived from molecular analysis we hope to improve our ability to resolve species relationships within Vermiculariinae. Morphological characters used include protoconch size, teleoconch whorl profile, growth line, sculpture, size, growth form, shell coloration, and hermatypic life mode. Several states were evaluated both early and late in ontogeny, with adult apertural whorls of regularly coiled turritellids compared to the late uncoiled whorls of vermicularine species. Previous researchers have distinguished the apical, coiled portion of the shell from the uncoiled/openly-coiled portion by referring to the "Turritella stage or turritellid stage", but we find this use clumsy (as by any monophyletic definition, Vermicularia *are always* turritellids) and here distinguish the apical "turritelliform" portion from the "vermiform" portion. Characters specifically related to uncoiling were coded as unknown character states for regularly coiled turritellid species, except that the number of of whorls before uncoiling was considered an ordered character with species that remain coiled coded as state 0 and species with 6 or fewer regularly coiled whorls coded as state 3. Character state descriptions and the character matrix is available in appendix 2.

Phylogenetic Methods

Parsimony analysis of both molecular and morphological characters was performed in PAUP4 (Swofford, 2003). Likelihood analysis was performed using RAxML (Stamatakis, 2006) under a GTRGAMMA model to calculate the ML best tree and 100 bootstrap replicates. Trees were visualized on FigTree v. 1.4.3 (Rambaut, 2016). Bayesian analysis was performed using BEAST v1.8.0 (Drummond and Rambaut, 2007) with Batillariidae designated as a monophyletic outgroup, using 10 million generations, with the first 10% of results discarded as burn-in. Morphological trees used

Turritella altilira (Miocene), *T. exoleta*, *T. acropora* and *T. nodulosa* as taxa representative of typical turritellid morphologies, with *T. nodulosa* and *T. acropora* chosen as out-group based on the molecular analysis conducted herein. Equal weighting was used as simulation data suggests that equally weighted analyses are more conservative in their estimation of tree topologies then parsimony analyses using implied weighting (Congreve and Lamsdell, 2016).

RESULTS

All molecular analyses recovered a monophyletic *Vermicularia* sister to a clade of *Turritella exoleta* + *Turritella clarionensis*. This clade was more closely related to the West and Southern African clade of *Protomella capensis* and *Turritella nivea* than other western Atlantic or tropical eastern Pacific turritellids with high bootsrap support or posterior probabilities. Parsimony placed *V. lumbricalis* (*knorrii*) as sister to *V. spirata* (Figue 2.4). The tree with the single best likelihood score placed *V. pellucida* as sister to *V. lumbricalis* (Figure 2.5), but a 70% majority-rule consensus tree was unable to resolve a polytomy among *Vermicularia* species (Figure 2.6). *V. spirata* was recovered as sister to *V. lumbricalis* with 0.99 posterior probability in Bayesian analysis, consistent with parsimony analysis (Figure 2.7). Consistent with Lieberman et al. (1993), Turritellinae sensu Marwick (1956) is paraphyletic with respect to *Vermicularia*. Parsimony analysis of morphological characters recovered a tree consistent with the molecular analysis for species with molecular data (*knorrii* as sister to *spirata*, in a monophyletic *Vermicularia* with *V. pellucida*, which is sister to *Turritella exoleta*; Figure 2.8). Tree topology was robust to the removal of *V. milleti*, *V. spirata radicula*, or both from the analysis (*V. radicula* being considered a duplicate species of *V. spirata spirata*, and *V. milleti*'s stratigraphic occurrence making this highly derived phylogenetic position unlikely; see discussion below).

Additional results of the molecular analysis include identification of *Mesalia* as a well supported clade, as is *Turritella* s.s. (*T. terebra* + *T. bacillum*). *Zaria duplicata, Maoricolpus roseus,* and *Protomella capensis* all show considerable molecular distance from their sister taxa, supporting the potential for these genera to carry meaningful phylogenetic information; however non-*Vermicularia* Turritellidae clearly require a revision beyond the scope of this paper.

Morphological analysis recovered a monophyletic *Vermicularia*, with *C. gracile* and *V. milleti* nested well within the clade. Adding geographic and stratigraphic ranges to the cladogram (Figure S2.1) suggests an alternative interpretation of tree topology (Figure 2.9) is more likely to be correct (Jackson and Cheetham, 1994). Excluding *V. milleti* from the analysis does not otherwise alter the topology of the tree. Here we presume *V. trilineata* to be synonymous with *V. weberi*, which extends the range of *V. weberi* into the latest Miocene – earliest Pliocene. Reports of *V. woodringi* in Jamaica (e.g., Olsson and Harbisson, 1951) are likely *V. katiae*, and are earliest Pliocene, not Miocene. There is a single specimen of *V. weberi*, UF 45471, listed as occurring in the Miocene Chipola Member of the Alum Bluff Formation, a stratigraphic assignment that is almost certainly an error for the overlying Pliocene Jackson Bluff member, in which *V. weberi* frequently occurs. If this stratigraphic assignment is correct, nearly all species would have extremely long ghost ranges during a time period that is richly fossiliferous in the American Neotropics (Figure S2.2). Given the excellent fossil record of marine gastropods at this time and the high incidence of convergence in whorl profile and sculpture known to occur in Turritellidae among basins (e.g., Allmon, 1994, 1996), we choose to remain agnostic with respect to the relationship between the middle Miocene European *V. milleti* and the other *Vermicularia* when interpreting the diversification of the rest of this principally Neotropical American clade (following the similar treatment of cheilostome bryozoans by Jackson and Cheetham, 1994)(Figure 2.9).

The sister relationship between the western Atlantic *V. woodringi* and Eastern Pacific *V. frisbeyae* implies a cladogenetic event prior to the closure of the Central American Seaway in the mid-Late Pliocene (Figure 2.9), and suggests the possibility of an unnoticed tropical eastern Pacificfossil record for *Vermicularia*, a conclusion also supported by the long ghost range in the morphological tree and substantial molecular divergence of *V. pellucida* from the clade of *V. knorrii* + *spirata*. Most species originated by cladogenesis rather than anagenesis (determined by co-occurrence of sister species or presumed ancestor-descendent lineages in time) with rapid diversification implied to have occurred in the latest Miocene or earliest Pliocene generating at least 7, possibly 8 lineages.

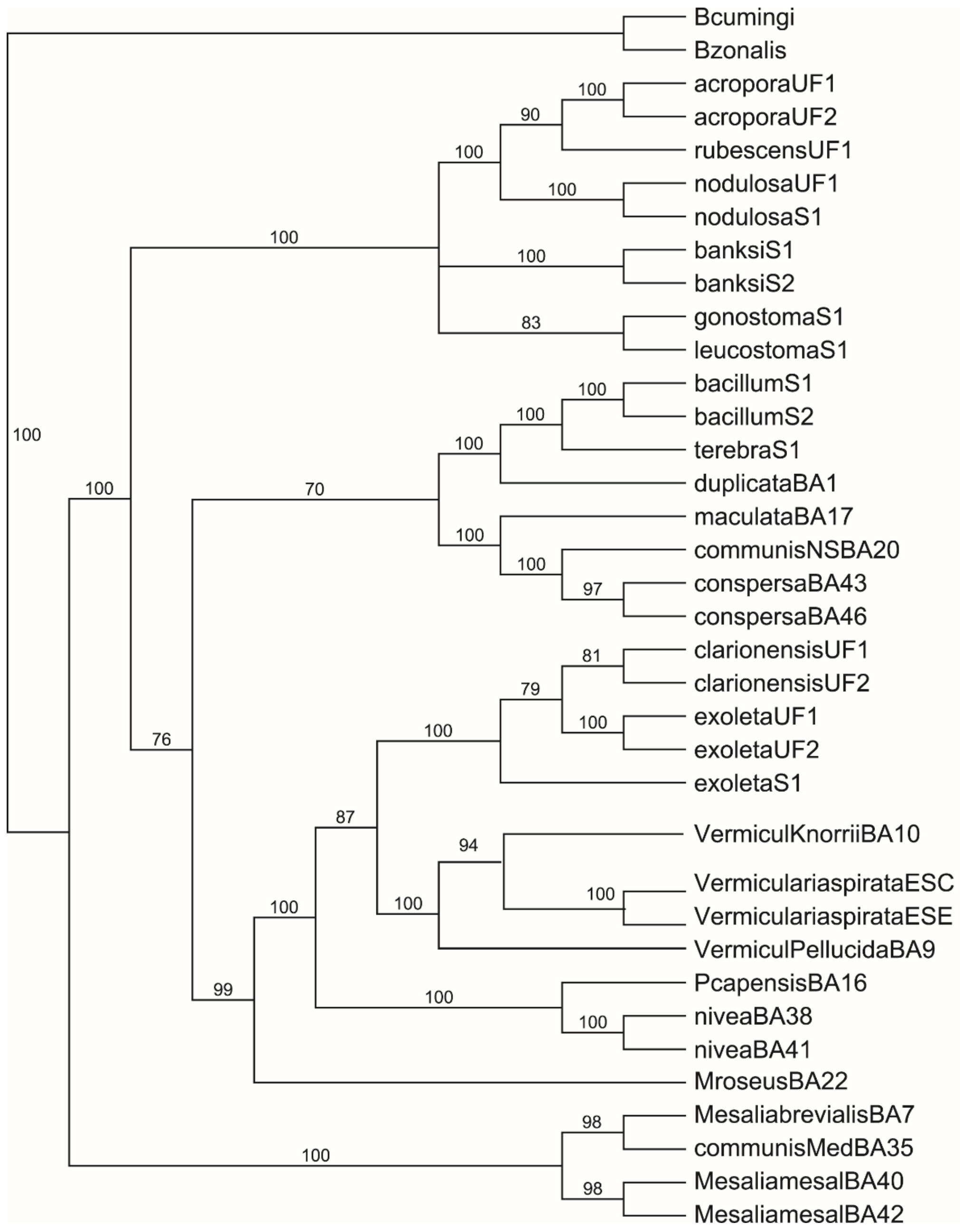


Figure 2.4. Parsimony analysis performed in PAUP4 of concatenated molecular dataset showing the 70% majority rule consensus tree of 100 trees, with numbers on nodes indicating bootstrap support.

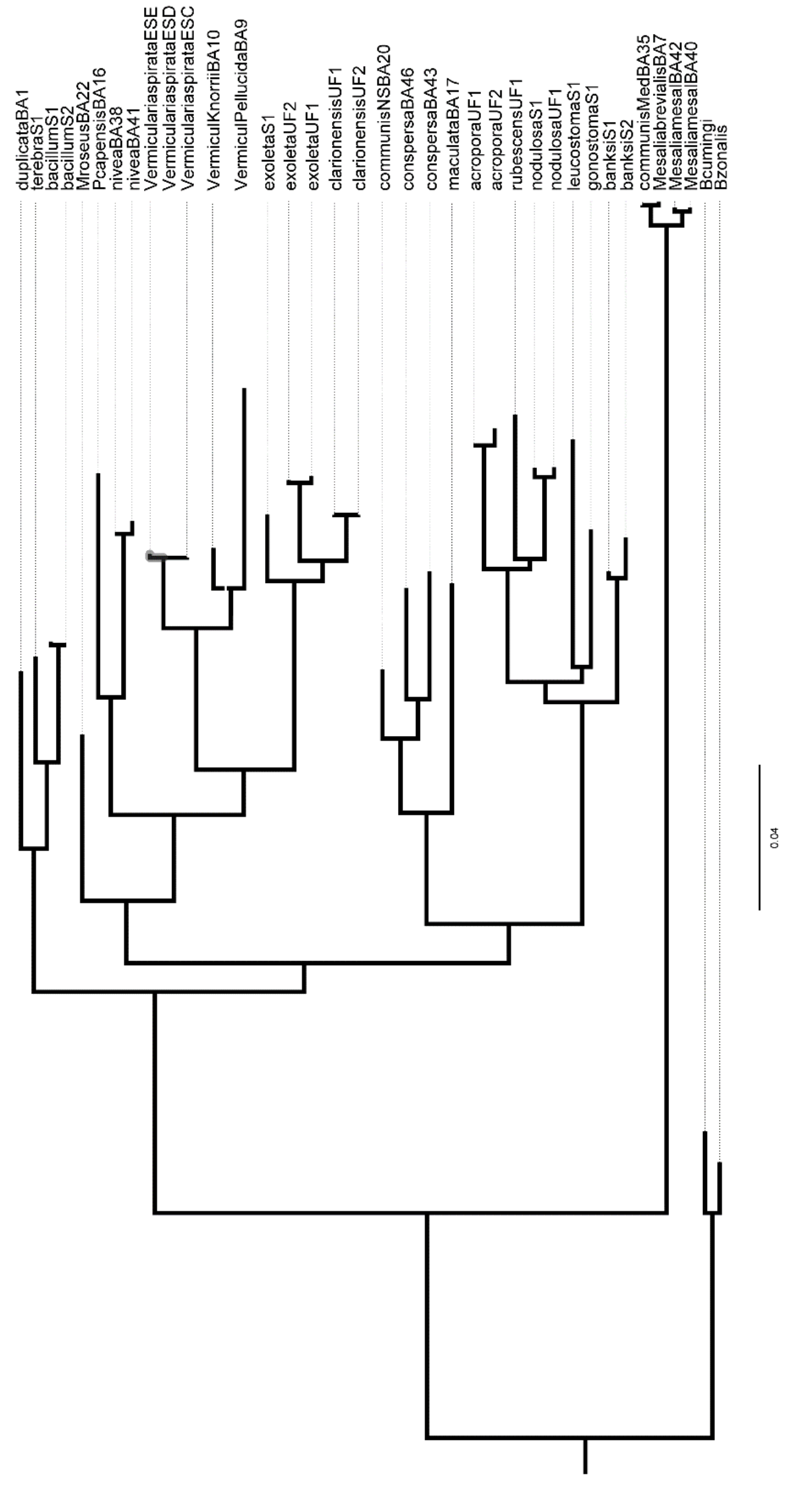


Figure 2.5. Single best ML tree reconstruction based on analysis of concatenated molecular dataset in RAxML.

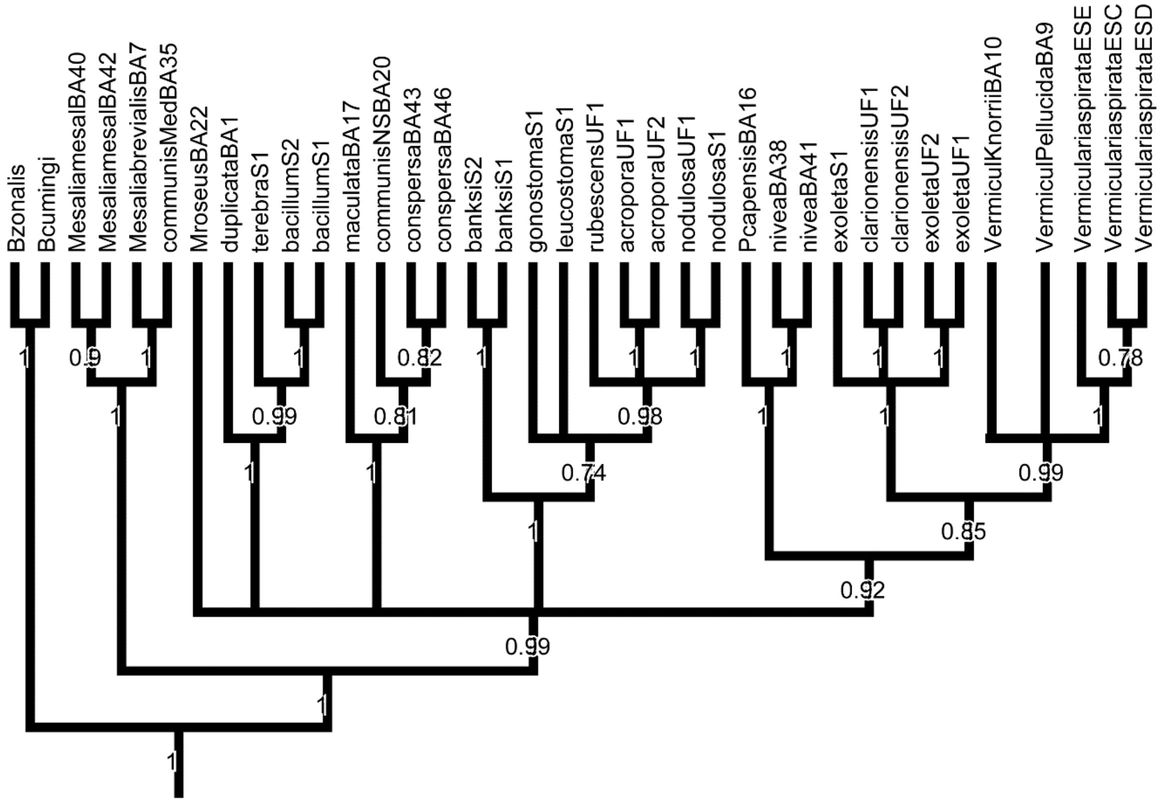
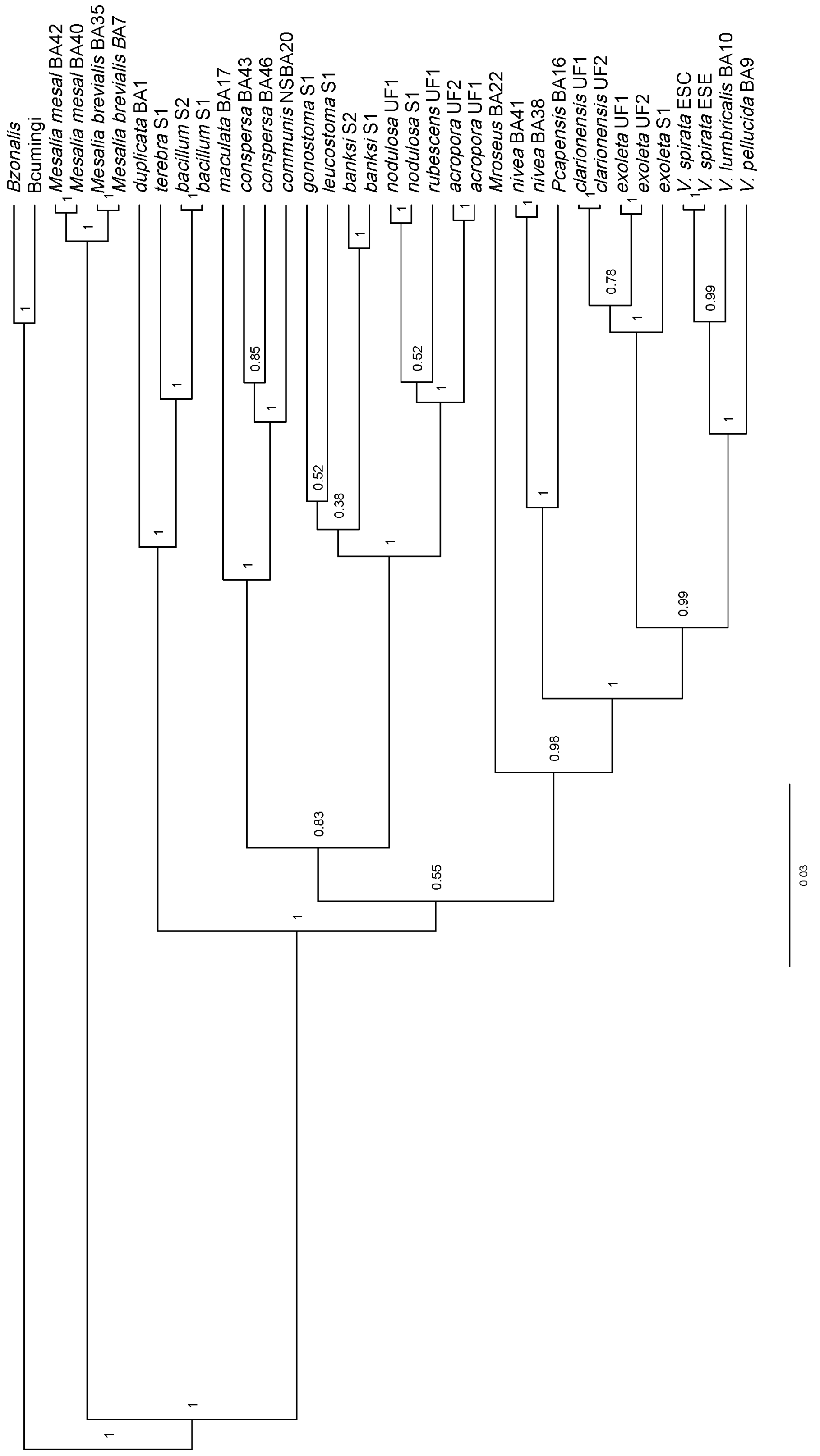


Figure 2.6. ML analysis, 70% Majority rule RAxML tree of 100 trees. Node values indicate bootstrap support.

Figure 2.7. Bayesian phylogenetic reconstruction generated using BEAST v. 1.8.0 based on the concatenated molecular dataset. Node values indicate posterior probabilities.



Bzonalis
Bcumingi
Mesalia mesal BA42
Mesalia mesal BA40
Mesalia brevialis BA35
Mesalia brevialis BA7
duplicata BA1
terebra S1
bacillum S2
bacillum S1
maculata BA17
conspersa BA43
conspersa BA46
communis NSBA20
gonostoma S1
leucostoma S1
banksi S2
banksi S1
nodulosa UF1
nodulosa S1
rubescens UF1
acropora UF2
acropora UF1
Mroseus BA22
nivea BA41
nivea BA38
Pcapensis BA16
clarionensis UF1
clarionensis UF2
exoleta UF1
exoleta UF2
exoleta S1
V. spirata ESC
V. spirata ESE
V. lumbricalis BA10
V. pellucida BA9
0.85
0.52
0.52
0.38
0.78
0.99
0.99
0.83
0.55
0.98
0.03

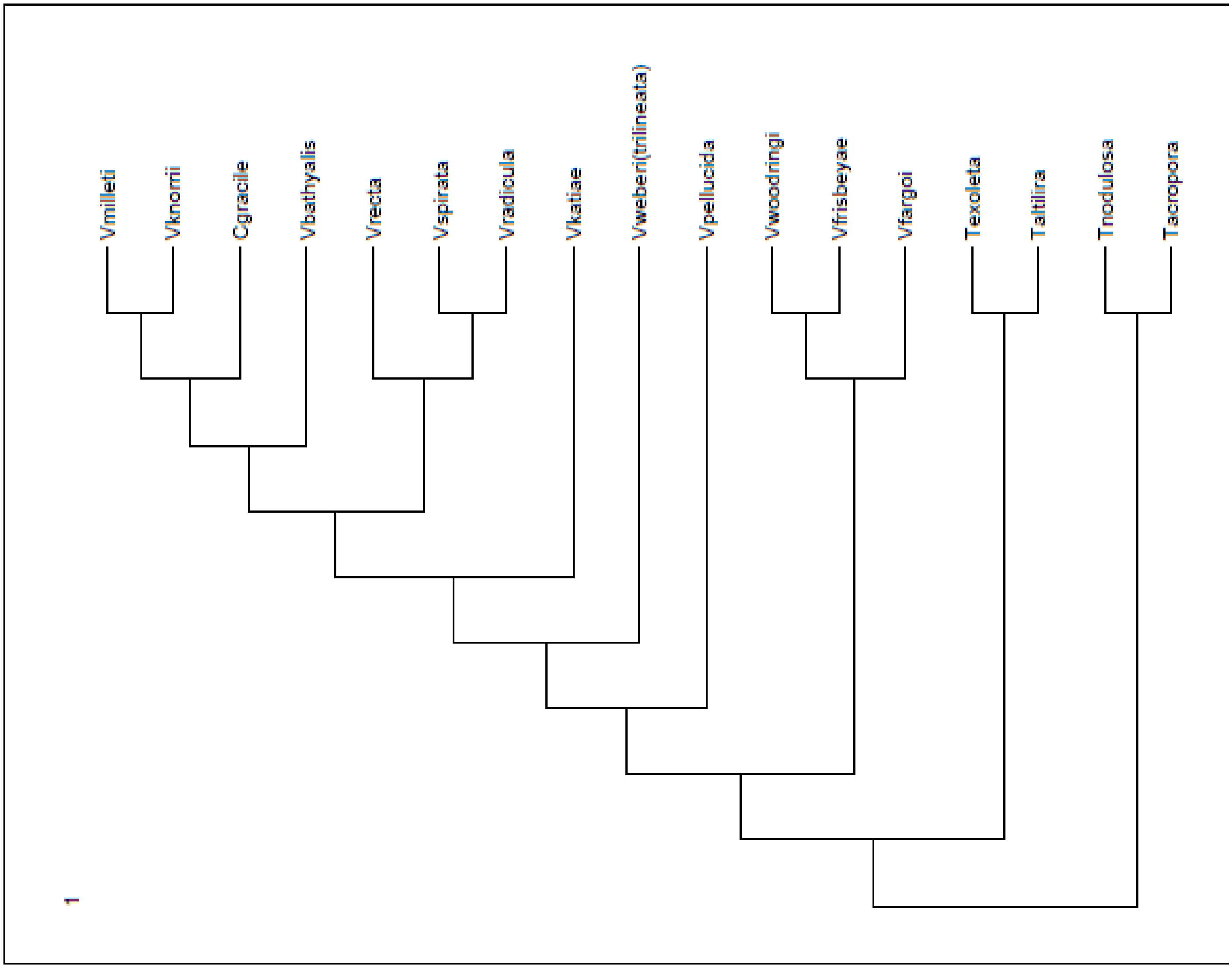
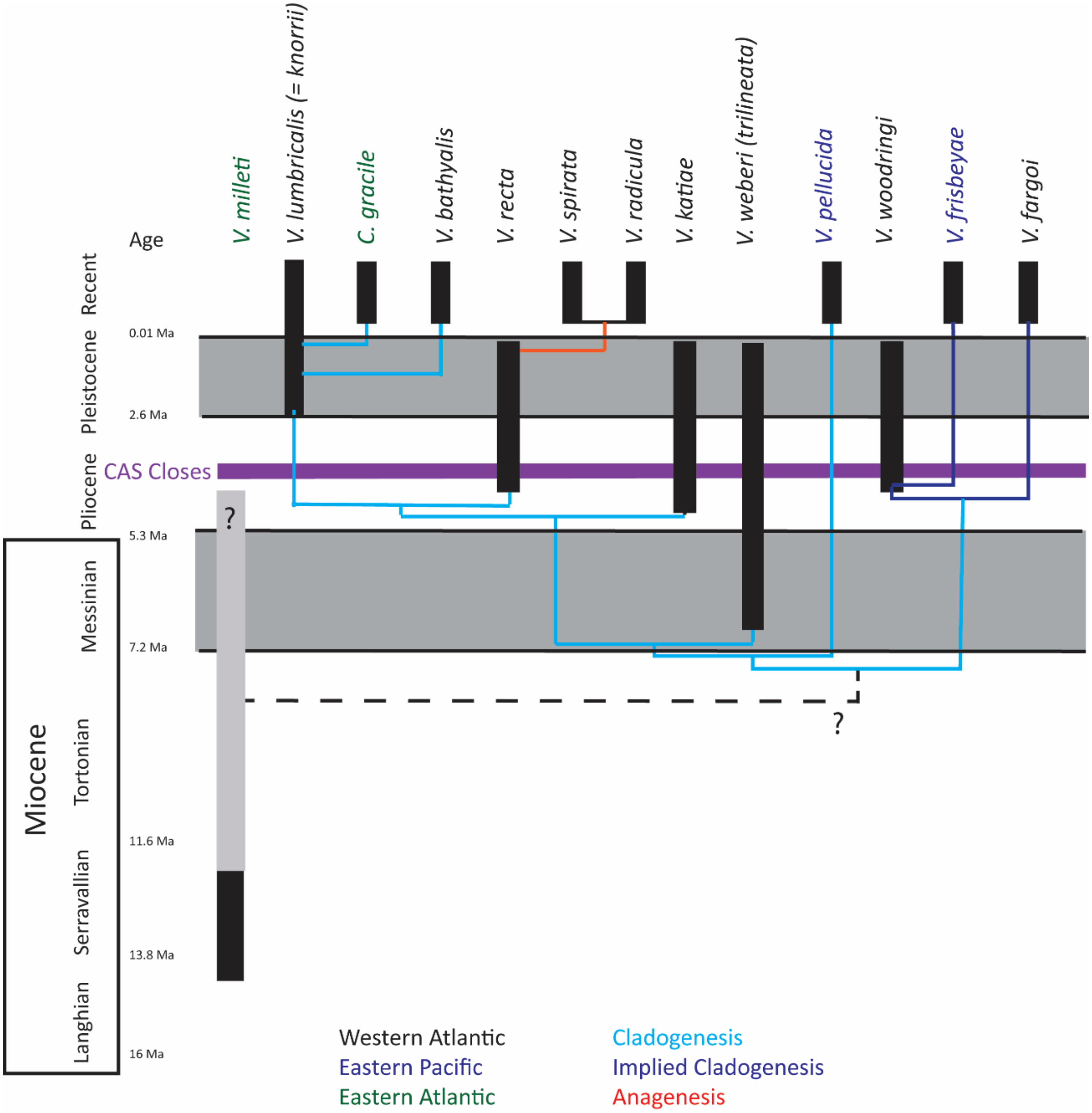


Figure 2.8. Maximum parsimony tree of Vermiculariinae species generated in PAUP based on morphological characters, using *Turritella nodulosa* + *Turritella acropora* as a monophyletic outgroup.

Figure 2.9. Phylogeny of fossil and extant *Vermicularia* showing the fossil record of each species (solid bars) minimizing ghost ranges in the richly fossiliferous Plio-Pleistocene of the Western Atlantic. As Eastern Pacific species could not have originated from Western Atlantic species after closure of the Central American Seaway, *V. frisbeyae* and *V. fargoi* must have ghost ranges extended prior to 3.5 Ma. V. milleti has been reported in the Pliocene of Spain, but was unfigured and it is therefore unclear whether this represents a true occurrence of *V. milleti*, an undescribed Vermicularia species in the *V. milleti* lineage, or another uncoiled gastropod.


V. milleti
V. lumbricalis (= knorrii)
C. gracile
V. bathyalis
V. recta
V. spirata
V. radicula
V. katiae
V. weberi (trilineata)
V. pellucida
V. woodringi
V. frisbeyae
V. fargoi
Age
Recent
0.01 Ma
Pleistocene
2.6 Ma
Pliocene
CAS Closes
?
5.3 Ma
Miocene
Messinian
7.2 Ma
Tortonian
?
11.6 Ma
Serravallian
13.8 Ma
Langhian
16 Ma
Western Atlantic
Eastern Pacific
Eastern Atlantic
Cladogenesis
Implied Cladogenesis
Anagenesis

DISCUSSION

Grabau (1907) hypothesized the paraphyly of the genus *Turritella* with respect to Vermicularia, but also the possibility that *Vermicularia* was paraphyletic. Molecular and morphological cladistic analyses herein support the monophyly of *Vermicularia*. Lieberman et al. (1993) used a partial sequence of 16S to study turritelline relationships, and determined that the genus *Turritella* as paraphyletic with respect to both *Vermicularia* and *Maoricolpus*, but identified these as sister taxa, with this clade sister to a clade consisting of *T. anactor* and *T. communis.* Our analysis of H3, 12S, and 16S for 3 *Vermicularia* species and a much expanded turritellid dataset confirms the monophyly of *Vermicularia* and Turritellinae as paraphyletic with respect to *Vermicularia*.

Uncoiling in the *Vermicularia* is principally accomplished by increasing translation rate (Raup's T) and altering the angle of the coiling axis, although many species become umbilicate prior to opening coiling (increasing Raup's D; Raup, 1966). By deflecting the coiling axis anteriorly separation of whorls is inevitable as growth is now tangential to the original axis of coiling. As umbilicate turritelliform stages are the primitive state for the *Vermicularia* (present in the *V. fargoi* + *V. woodringi* clade, *V. pellucida,* and *V. katiae*), ontogenetically earlier deflection of the coiling axis may have eliminated the umbilicate whorl in the *V. lumbricalis* + *V spirata* clade.

Several taxonomic notes should be attended: *Vermicularia lumbricalis* appears to be the senior synonym of *Vermicularia knorrii*. *Vermicularia trilineata* Guppy 1864 may be the senior synonym of *V. weberi*, but the lectotype material of *V. trilineata* is of poor quality. While consistent with *V. weberi*, not all characteristics of *V. weberi* can be confirmed as present in Guppy's material of *V. trilineata*, although the specimens do appear to be *Vermicularia* (initiating uncoiling) rather than *Turritella* as suggested by Olsson and Harbisson (1953). *Vermicularia radicula* type material unfortunately appears to have been destroyed, but material collected at the type locality, Vinyard Sound, Mass. (USNM 74788 here designated as lectotype) falls within the typical range of variation of *Vermicularia spirata*. They may be more likely to have beaded spiral cords, a feature shared by the extirpated Walsingham Pond population of *V. spirata*, more frequently exhibit pinkish-dark reddish-brown coloration, and no large (>5 cm length) specimens were encountered, so retention of this name as a subspecies of *Vermicularia* restricted to waters North of Long Island is justified.

The three subspecies of *Vermicularia fargoi* listed in (Petuch and Myers, 2014) are likely valid. *Vermicularia fargoi* is recovered as basal to the remaining *Vermicularia* in morphological analysis. No specimens could be obtained for molecular analysis although this species is extant. If this placement is correct the undetected Miocene-Pliocene ancestors of *V. fargoi* may have been regularly coiled, indicating parallelism in the evolution of openly coiled morphology in the *Vermicularia*.

It is notable that hermatypy is hypothesized to have evolved twice in *Vermicularia*, in the *recta-spirata* lineage and *V. woodringi*, a case of parallelism within *Vermiculara* (gregariousness and cementation to hard substrate likely predisposed the group to this habit) and convergence with reef-forming vermetids.

An unexpected result was the recovery of the Eastern Atlantic species *Callostracum gracile* and *Vermicularia milleti* in a clade with *Vermicularia lumbricalis*. While both *lumbricalis* and *C. gracile* are modern species, with lumbricalis being broad-ranging (confirmed as far East as Bermuda) making this placement reasonable for *C.*

gracile, we urge caution regarding the interpretation of *V. milleti*, the oldest *Vermicularia* species (~13 Ma), as it implies substantial ghost ranges across the tree. In the absence of molecular evidence, definitively assigning *C. gracile* to a group other than *Vermicularia*, the placement of *C. gracile* within the phylogeny suggests it should be moved to *Vermicularia*.

V. milleti represents an interesting morphological experiment. Unlike *Delphinula conica*, it has typical turritellid growth lines (*Delphinula conica* possesses nearly straight growth lines; Lozouet 2012) and whorl morphology/sculpture consistent with other *Vermicularia*. Given the phylogeny, 3 hypotheses are possible.

1. It truly is sister to *V. knorrii* lineage and all major *Vermicularia* lineages originated in the Miocene.

2. *V. milleti* properly belongs to *Vermicularia*, but diverged from the western Atlantic clade prior to its Pliocene expansion and *V. knorrii* converged on similar whorl profile and sculptural morphology.

3. *V. milleti* independently converged on uncoiled morphology and either belongs to the clade consisting of *Vermicularia* and stem-group normally coiled turritellids in the *Vermicularia* lineage or developed uncoiled morphology completely independently of the *Vermicularia* clade.

Hypothesis 1 seems unlikely given the exceptionally good record of Miocene Turritellidae of the Western Atlantic coastal plains. Hypothesis 2 is tentatively supported by the monophyly of *Vermicularia* for which molecular data was available, the consistency of characters such as basal sinus and lateral sinus with other *Vermicularia*, the reasonably deep divergence time indicated by the ML and Bayesian trees, and the long fossil record (at least Eocene) of the sister group leading to *Turritella (Torcula) exoleta* (*Torcula martinensis*; PaleoDB collection 92785, Authorized/entered by Austin Hendy from USNM). If *V. milleti* did in fact persist through the Pliocene, as reported in La Perna et al. (2001), then this would seem to be the most likely scenario according to stratigraphic and geographic occurrences – a single Late Miocene dispersal event to the Western Atlantic from a persistent population of *V. millet*i or a species in the *V. milleti* lineage. If molecular data were obtained for *V. gracile* and these indicated repeated independent origins for uncoiled morphology in turritellids, hypothesis 3 would need to be more thoroughly explored. A rigorous phylogeny incorporating all fossil turritellids from the Paris Basin, West Africa, the American Neotropics and including *Mesalia* is necessary to have high confidence that *V. milleti* properly belongs to *Vermicularia* (hypothesis 3), but at present it is not known which shell characters are most likely to correspond to phylogenetic hypotheses consistent with molecular analyses. Further analysis of turritellid molecular data is needed in order to determine both the frequency of trans-Atlantic dispersal and evaluate the frequency of convergence in various types of shell characters.

CONCLUSIONS

Vermiform morphology evolved several times in Gastropoda (Morton, 1953; 1955; Bieler, 1996; Bieler and Petit, 2011; Bandel and Kowalke, 1997), in Vermetidae, Siliquariidae, and Turritellidae, as well as the campaniloid *Delphinula conica* (Lozouet, 2012), the murchisoniid *Loxoplocus* (Peel, 1975), the prosobranch *Helminthozyga* (Peel, 1975), and at least once in Turritellidae.

The taxonomic and geographic expansion of *Vermicularia* species in the Pliocene and Recent of the Americas is an interesting evolutionary event, especially as non-*Vermicularia* turritellids exhibited a significant reduction in species diversity after the Pliocene closure of the Central American Seaway (Allmon, 1992b, 2001). As *Vermicularia* are properly assigned to the turritellids, the decline in turritellid species number (though still dramatic) is typically overestimated. Representing 4 of 7 species, most Recent Western Atlantic turritellids are *Vermicularia*. *Vermicularia*, like tetrapods within the sarcopterygians (Greene, 2001), represent diversity that is not generally appreciated because the clade is so highly derived it is readily apprehended as different (e.g., when asked how many dinosaurs are found in New York, we typically reply none, ignoring the substantial avian population). Like Edmond Dantès in the Count of Monte Cristo, they have so thoroughly transformed themselves that they are only recognized by those with special familiarity with the group. Such highly derived 'Monte Cristo taxa' represent opportunities for educating students or the public about how evolutionary relationships are hypothesized and tested, and how apparently dramatic evolutionary changes are accomplished.

As we have conducted a complete review of a clade, we are also able to test the evolutionary mode (anagenesis or cladogenesis; see Allmon, 2017) associated with morphological change (Jackson and Cheeham 1999). The phylogeny (Figure 2.9) indicates that 9/10 species originated by cladogenesis (as determined by ancestral persistence ((Gould, 2001), with *V. spirata* possibly derived from *V. recta* by anagenesis. Biogeography suggests that both *V. bathyalis* and *V. gracile* likely both originated separately by allopatry from *V. lumbricalis*, resulting in a true (hard) polytomy even though resolution is achieved in the MP analysis (Hoelzer and Meinick, 1994). Reports of *V. spirata* in the Plio-Pleistocene do not appear to be accurate (consistent with the observations of Olsson and Harbisson, 1953), and suggests a completely cladogenetic history for *Vermicularia* species, if confirmed. The history of this clade thus supports the hypothesis of punctuated equilibria (Eldredge and Gould, 1972; Gould and Eldridge, 1977), contradicting Erwin and Anstey, (1995), but consistent with Prothero (1992), Jackson and Cheetham (1999), Gould (2002), and Friend and Allmon (in review). This diversification and the ontogenetic mechanisms that resulted in this unusual morphology of this group are also worthy of further examination.

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***Smithia gracilis* Maltzan, 1883**, NHMUK 1909.7.27.1. Images are copyright of the Natural History Museum of London and if published they must be quoted as such; these images were taken by Kevin Webb, NHMUK Photographic Unit.

SYSTEMATIC DESCRIPTIONS

Nomenclature for morphological characters is detailed in appendix 2, and follows Allmon, 1996 and the elaboration in Sang et al. (in review) for general turritellid characters. Due to widespread confusion regarding the application of species names, synonymy lists are not exhaustive, but rather reflect only cases where the species were illustrated, or where corresponding specimens were examined. The admixture of multiple species in photographs or lots of *Vermicularia* species, particularly *spirata* or *knorrii* also complicates synonymy lists, especially for sources such as shell identification guides. Distribution information was derived from observed specimens at the collections of PRI, LACM, USNM and UF, combined with information from original descriptions, and in literature where specimens were illustrated or described in sufficient detail to confirm species identities. Distribution information should therefore be treated as a conservative estimate for all species.

Table 2.2. The following species are considered to be valid members of the genus *Vermicularia.*

Vermicularia bathyalis	Petuch, 2002
Vermicularia fargoi	Olsson, 1951
Vermicularia frisbeyae	McLean, 1970
Vermicularia gracilis	Maltzan, 1883
Vermicularia katiae	n.sp.
Vermicularia lumbricalis	Linnaeus, 1758
Vermicularia pellucida	Broderip and Sowerby, 1829
Vermicularia recta	Olsson and Harbisson, 1953
Vermicularia spirata	Philippi, 1836
Vermicularia weberi	Olsson and Harbisson, 1953
Vermicularia woodringi	Olsson and Harbisson, 1953

Turritellidae Lovén, 1847

Vermiculariinae Dall, 1913

Synonymy: Vermiculariidae Dall, 1913a

Type: *Vermicularia* Lamarck, 1799

Remarks: Dall (1913a) removed *Vermicularia* from Vermetidae, erecting Vermiculariidae, while Morton (1953) subsequently recognized Vermiculariinae as a subfamily within Turritellidae. The subfamily is occasionally incorrectly reported as being proposed first by Dall (1913)b; the correct reference is Dall, (1913a, p. 546).

Vermicularia

Synonymy: Vermicularia Lamarck, 1799

Type: Serpula lumbricalis Linnaeus, 1758

Remarks: Bieler and Petit (2011) note that *Serpula lumbricalis* Linnaeus, 1758 referred to four illustrations, all within the modern *Vermicularia*, and that the locality given as “habitat in Indiis” is in error, as t *Vermicularia* are an Atlantic and Tropical Eastern Pacific group. See Bieler and Petit (2011) and Keen (1961: 186-188) for additional details on the history of the type species of this genus.

Vermicularia bathyalis

Synonymy: Vermicularia bathyalis Petuch, 2002

Types: Holotype UF 277097; paratype UF 279230

Material examined: USNM 1138077 (2 specimens; material identified by original author)

Diagnosis: Most similar to *V. lumbricalis*, turritelliform portion has fewer whorls, uncoiled portion has more, finer spiral cords while *V. lumbricalis* has 2 stronger cords that weaken as the shell lengthens, and *lumbricalis*’ whorl profile is more rounded.

Description: Protoconch unknown. Average size for the genus; coiling loosens at last turritelliformwhorl before becoming uncoiled after ~4 whorls. Apex light colored, beginning to darken in last turritella-stage whorl. Uncoiled portion has reduced spiral sculpture but has a scaly/wrinkled appearance. Aperture of uncoiled portion rounded. Whorl profile frustrate. Turritelliform portion keeled. 12 faint, evenly spaced spiral cords on uncoiled portion. Basal Sinus Allmon type 1. Lateral sinus medium depth, straight inclination, no major inflection points, with the apex located on the upper third of the shell.

Distribution: Recent. Deep water (400-600 m), presently known only from the Bahamas, East of the FL straights

Vermicularia fargoi

Synonymy: 3 valid subspecies; *V. fargoi fargoi,* Olsson, 1951 (western Florida)*, V. fargoi owensi* Petuch and Myers, 2014, and an unnamed third subspecies occurring in Texas identified by Petuch and Myers (2014) as illustrated in Tunnell et al. (2010).

Types: Holotype ANSP 187640*; V. fargoi owensi* holotype- USNM 1231410;

Material examined: ANSP 187640 *V. fargoi owensi* type- USNM 1231410; UF 277956

Diagnosis: Large turritelliform stage. Similar to the Pacific *V. frisbeyae*, but *V. fargoi* has 3 prominent spiral cords while *V. frisbeyae* has only 2.

Description: Protoconch unknown. Largest turritelliform portion among *Vermicularia*. Whorl profile frustrate. 2 prominent spiral cords above and below midpoint of the whorl, with a third slightly weaker, but still prominent cord near the top of the whorl. Sculpture commonly beaded. Umbilicate. Basal Sinus Allmon type 2, Lateral Sinus medium, prosocline, no significant inflection points, apex at the midpoint on the whorl. Aperture quadrate.

Distribution: Recent. 0-10 m depth. Cuba, Florida-Texas.

Remarks: Subspecies variable in pleural angle. *V. fargoi owensi* appears to only have 2 uncoiled whorls, while *V. fargoi fargoi* typically undergoes a gradual separation of whorls and takes on a more vermiform appearance late in ontogeny. Specimens may change their coiling axis, but it is notable that they often do not, or remain close to the coiling axis of the turritelliform portion. Although listed as common in Olsson (1951), we were unable to locate a living individual for molecular analysis.

Vermicularia frisbeyae

Synonymy: Vermicularia frisbeyae McLean, 1970;

Types: Holotype LACM 1278; paratype LACM 1279

Material examined: LACM 1278; LACM 1279

Diagnosis: Only 2 modern species of *Vermicularia* occur in the Eastern Pacific, *V. pellucida* and *V. frisbeyae*, with *V. frisbeyae* possessing a substantial turritelliform stage. Compared to *V. fargoi*, which also has an extended turritelliform stage, *V. frisbeyae* possesses only 2 prominent spiral cords while *V. fargoi* has 3.

Description: Protoconch unknown. Large turritelliform stage, ~12 teleoconch whorls. Earliest teleoconch cream colored. Darker patches give the later whorls a roughly striped appearance, which can make sculpture appear lightly beaded, but it is smooth on the type and paratype. Whorl profile flat sided. Sculpture consists of two strong cords initially even in strength with the top (posterior) cord, reducing in strength later in ontogeny, but the D (sutural) cord becoming more prominent. Turritelliform portion umbilicate before uncoiling. Vermiform portion not present in type, but described by McLean (1970) as opening for a complete volution, and then producing 2 more whorls at a 45-degree angle to the initial coiling axis. McLean described the uncoiled specimen as 61.2 mm in total length, approximately half of that length belonging to the uncoiled portion. Basal sinus Allmon type 5. Lateral sinus deep, opisthocline, single inflection on top, apex in the middle third of whorl.

Distribution: Recent. Eastern Pacific; southern Mexico to western Panama.

Vermicularia gracilis

Synonymy: *Callostracum gracile* Smith, 1909:229; *Smithia gracilis* Maltzan, 1883:97-98

Types: Holotype *Smithia gracilis* Maltzan 1883; Neotype NHMUK 1909.7.27.1

Material examined: NHMUK 1909.7.27.1

Diagnosis: It is notable in its consistent retention of the same coiling axis despite whorls becoming detached, its rounded whorl profile, and its complex coloration pattern compared with other members of the genus. Only *V. fargoi* also frequently maintains an open coiled portion close to retaining the original coiling axis, and *V. fargoi* has a much larger coiled stage along with pronounced spiral sculpture with 3 primary spiral ribs. The rounded whorl profile also readily distinguishes *V. gracile* from *V. knorrii*, which has a strongly carinate whorl profile.

Description: Protoconch paucispiral, nucleus slightly submerged, approximately 350-375 µm. Whorls become detached after 2 or 3 volutions, but maintains coiling axis. Early whorls white to cream colored, later whorls dark, with light maculations. Aperture teardrop shaped. Whorl profile convex. Sculpture consists of many fine spiral lineations of approximately equal strength. Lateral Sinus medium depth, opisthocline, no significant inflection points, apex on upper third of whorl.

Distribution: Recent; Senegal; introduced in western Mediterranean

Remarks: The only eastern Atlantic *Vermicularia* species presently known. Marwick (1956) noted that Wenz (1939) classed Callostracum as a subgenus of Mesalia, but Marwick considered it to be turritelline, as it lacks a truncated columella, effuse aperture and the operculum is more similar to *Turritella* than *Mesalia*.

Vermicularia katiae n.sp.

Synonymy: New species

Types: Holotype PRI 76997; paratypes PRI 68759; UF 132812

Etymology: “Katie’s worm snail”, named for Katherine Mary Anderson, the spouse of BMA

Material examined: PRI 76997 paratypes PRI 68759, UF 132812

Diagnosis: Unlike *V. woodringi* the species has only one truly prominent spiral cord, just below the midpoint on the whorl, with a secondary noticeable but much weaker cord above. Whorls ae hypercampanate, distinguishing the species from *V. lumbricalis.*

Description: Protoconch unknown, implied to be smaller than 350 µm from 360 µm early teleoconch whorl. Small, uncoiling early in ontogeny (~5-6 whorls). Whorls hypercampanate. 2 main spiral cords, with the adapertural cord forming a prominent keel. Turritelliform portion umbilicate. Basal sinus Allmon type 1. Lateral sinus deep, opisthocline, single inflection on bottom, apex on upper third of whorl.

Distribution: Pliocene-Pleistocene. Type locality Gurabo Formation (Pliocene), Dominican Republic; banks of the Rio Gurabo, Vokes localities 1277 and 1210 (above and below ford of the Los Quemados-Sabaneta road (1976-77), (see also Saunders et al., 1986)). Also known from the Falmouth Formation (Pleistocene), Jamaica.

Remarks: V. katiae is likely the source of much confusion regarding the distribution of *V. woodringi* in space and *V. lumbricalis* (*knorrii*) in time.

Vermicularia lumbricalis

Synonymy: Serpula lumbricalis (Linnaeus 1758); *Vermicularia lumbricalis* Lamarck 1799*, Vermicularius* Montfort 1810*, Vermicularia knorrii* Deshayes, 1843*, Vermetus knorrii* Deshayes 1843; *V. knorrii* Petuch, 2002; *V. knorrii* Petuch and Myers, 2014; *V. knorrii* Tunnell et al., 2010, 2014.

Types: Holotype UUZM Linneasmlingen 802

Material examined: UUZM Linneasmlingen 802, original Illustration from which *V. knorrii* was named (Knorr 1757) used as an informal "epitype" (an illustration or clarification of a type specimen) (Bouchet and Strong, 2010; Schrodi and Haszprunar, 2016); "*V. knorrii*" LACM 25985, "*V. knorrii*" PRI 73787, "*V. knorrii*" UF 446833

Diagnosis: It is notable for its smaller size (both in length and maximal width), consistent shift from light to dark color from early to later whorls, although the pigmented portion may range from tan to dark brown. Distinguished from *V. spirata* by its smaller size and 2 spiral keels which decrease in strength on the vermiform portion.

Description: Protoconch maximal width 350-400 µm. Turritelliform portion white, becoming much darker at uncoiling. Whorl profile campanulate. Typically uncoils from 4-6 whorls, but may have up to 8. 1 prominent spiral cord on turritelliform portion accentuating the keel, with a second more reduced cord also present . Vermiform portion has spiral cords may be greatly reduced, and may appear smooth or wrinkled. Basal Sinus Allmon type 1. Lateral sinus deep, opisthocline, no inflection points, apex located medially. Aperture circular.

Distribution: Pleistocene-Recent. Typically 2-50 m; but reported from up to 500 m (Tunnell et al., 2010), although it is possible that these specimens are in fact *V. bathyalis*. Texas to Florida, Antigua, Barbuda, Cuba, Jamaica, Atlantic coast from Florida to North Carolina, Bermuda.

Remarks: Vermicularia "knorrii" is among the most common *Vermicularia* present in collections, however it appears to be a junior synonym of *V. lumbricalis. V. knorrii* was originally described as being easily distinguished from *lumbricalis*, however the description by Deshayes (1843) implies that it is in fact being distinguished from *Vermicularia spirata* which has been misidentified as *V. lumbricalis*. Often found in sponges.

Vermicularia milleti

Synonymy: Deshayes 1839. *Vermicularia pseudoturritella* Boettger 1906 (nomen nudum) appears to refer to this species. *Vermicularia milleti* Landau et al. 2004

Types: No type material could be located.

Material examined: UF 230914

Diagnosis: Unlike *Delphinula conica* Lozouet 2012 (formerly *Vermicularia conica*), which has a campanilioid protoconch and growth lines lacking a lateral sinus, *V. milleti* appears to have genuine turritellid affinities.

Description: Small, 2-3 cm long, open coiling beginning after 7 whorls. Whorl profile campanulate. 3 spiral cords present on turritelliform whorls, the strongest forming a keel that is maintained on the openly coiled whorls. Whorl D cord (just above the suture) is minor on earliest teleoconch whorls, increasing in strength until disappearing at uncoiling. B cord begins nearly as prominent as C cord, but then fades in relative strength. Basal sinus Allmon type 1. Lateral sinus shallow, uninclined, single inflection point on top, apex on upper 1/3 of whorl.

Distribution: Middle Miocene Faluns de Touraine Fm, Paris Basin (Deshayes, 1839). Also reported in the middle Miocene of Hungary and Romania (Saint Martin et al., 2000). Reported in the Pliocene of Spain by La Perna et al. (2001), but was unfigured.

Remarks: See main text for a discussion of its taxonomic placement and implications.

Vermicularia pellucida

Synonymy: Vermetus pellucidus Broderip & Sowerby, 1829*; Vermiculus pellucidus; Vermicularia eburnea* (*Reeve, 1842), Vermetus fewkesi* Yates, 1890 *Vermicularia fewkesi* Yates, 1890. 2 valid subspecies *Vermicularia pellucida pellucida and*

Vermicularia pellucida eburnea Reeve 1842*. V. fewkesi* is a junior synonym of *Vermicularia pellucida eburnea.*

Types: Type material of Broderip and Sowerby, 1829 could not be located.

Material examined: LACM 1966-188, LACM 1972-85, LACM 1938-52, LACM 1933-170, UF 372362

Diagnosis: Smaller turritellid stage than *V. frisbeyae*, the only other Recent Eastern Pacific *Vermicularia*, and maintains 2 strong spiral cords throughout turritelliform stage, while the upper cord diminishes in strength in *frisbeyae*.

Description: Protoconch 300-350 μm in maximum diameter; Uncoiled portion often nearly planispiral which is unusual for the group, but may take on other forms. Can be large for the group, with apertural widths reaching ~1 cm. Whorl profile campanulate with 2 prominent spiral cords. The first teleoconch whorl appears medially keeled, but the posterior (more apical) spiral cord increases in prominence by the second teleoconch whorl and remains strong on the remainder of the turritelliform portion. Typically uncoils after 7-9 whorls, but may reach 9-10. 3 spiral cords present on vermiform portion of shell. Basal sinus Allmon type 1; lateral sinus medium depth, uninclined, possesses a single inflection point at the bottom of the whorl, with the apex of the sinus located medially.

Distribution: Recent. 10- 80 m water depth. Eastern Pacific, Southern California (Anacapa passage) to Peru and the Galapagos Islands

Remarks: Degree of pigmentation varies substantially from translucent to solid tan, with brown maculations commonly occurring on any background or not at all.

Vermicularia recta

Synonymy: Vermicularia recta Olsson and Harbisson 1953

Types: Holotype ANSP 18974

Material examined: ANSP 189974, PRI 73952, PRI 76998

Diagnosis: Individual specimens are very similar to the Recent *Vermicularia spirata*, it has a more rectilinear aperture and cross section, while *V. spirata* is nearly circular in cross section. When the turritelliform apex is not severely worn it displays much stronger spiral sculpture than *V. spirata*, with A, B, and C cords distinct on earliest whorls and D becoming more prominent in the last turritelliform whorls.

Description: Can reach the greatest lengths of known fossil *Vermicularia*. Occurs free, but often in lightly cemented intercoiled masses. Turritelliform portion approximately 8 whorls. Whorl profile frustate. Vermiform portion 200-300 mm long. Turritelliform portion with 3 (rarely 2) spiral cords, with a 4th (D) cord becoming stronger as the suture deepens before coiling opens. 2 strong medial spiral cords on vermiform portion which may fade towards the aperture but are detectible throughout ontogeny. Many minor spiral cords are present throughout ontogeny. Flattened on inner side of the whorl giving a more rectangular appearance to the aperture than *spirata*, which is circular in cross section. Basal sinus Allmon type 1. Lateral sinus medium depth, prosocline, uninflected, apex medially placed.

Distribution: Plio-Pleistocene of Florida. Bermont Fm., Caloosahatchee Fm, Taimiami Fm.

Remarks: V. recta forms prominent reefs which can be of stratigraphic significance. Often any substantial mass of intercoiled/cemented *Vermicularia* tubes is assigned to *V. recta*, but *V. woodringi* and *V. spirata* also form such associations. *V. recta* maintains a flattened inner coiling surface as opposed to a rounded one, and is generally larger in diameter at a given length than *V. woodringi*, which frequently co-occurs with *V. recta* and is misidentified as such.

Vermicularia spirata

Synonymy: Vermetus spiratus Philippi, 1836*; Vermetus bicarinatus* Deshayes, 1843*; Vermetus quadrangulus* Philippi, 1848; *Vermicularia radicula* Stimpson 1851; *Vermicularia spirata* Olsson and Harbisson 1953; Bieler and Hadfield, 1990.

Types: Holotype of *V. spirata* at the Zoologisches Museum, Humboldt Universitat, Berlin. Epitype figure from Philippi, 1836. Holotype of *V. radicula* destroyed in the 1877 Chicago fire (fide Warner, 2015). Neotype of *V. spirata radicula* designated here USNM 74788

Material examined: USNM 122207, USNM 435015, USNM 74788, USNM 463252, USNM 463252, USNM 776784, MCZ 382941

Diagnosis: Reaches the greatest lengths of any modern *Vermicularia* species, and is substantially larger in width at a given length than *V. lumbricalis (=knorrii)* the other wide-ranging Atlantic species. Possesses a less carinate whorl profile than *V. lumbricalis,* and maintains distinct spiral cords well into the uncoiled portion of the shell.

Description: Protoconch approximately 1.5 unsculptured whorls*.* Longest Recent species, up to 22 cm. Typically has a brief turritelliform stage of 7-9 whorls which is pigmented as the rest of the shell, but uncoiling whorl number is variable and may be ecophenotypic, proceeding once viable substrate is found. Whorl profile campanulate-frustate. Sculpture dominated by 2 strong medial cords, with a minor A cord the D cord increasing in prominence as coiling loosens. Spiral sculpture is typically smooth but may be beaded. Color is most commonly tan but ranges to reddish brown. Vermiform portion has many fine lineations. Basal sinus Allmon type 2. Lateral sinus shallow, uninclined, uninflected, apex medially placed. Aperture circular. Sculpture typically smooth, but beading is known to occur in specimens from throughout the range, especially in individuals of *V. spirata radicula* and some specimens from the Walsingham Pond population.

Distribution: Recent. Type locality Cuba. Belize, and Yucatan peninsula, Atlantic coast from Texas- Massachusetts, Bermuda. Carribbean including Barbuda, Dominican Republic, Trinidad, and Guyana.

Remarks: A principle reef former in the Carolinas, *V. spirata* is more typically found among corals, especially branching corals, although it may also be found associated with sponges, or in masses of conspecifics. *V. spirata* is the most widespread modern species. We concur with Olsson and Harbisson (1953) that this is an exclusively modern species.

Vermicularia weberi

Synonymy: Vermicularia weberi Olsson and Harbisson 1953*.* Existing type material of *V. trilineata* Guppy 1867 is consistent with *V. weberi*, implying synonymy with *Vermetus trilineatus* Guppy 1867 (Not *Vermicularia spirata* var. *trilineata* Guppy 1925)

Types: Holotype ANSP 17370; lectoype of *V. trilineata* USNM 645365

Material examined: ANSP 17370, Lectotype of *V. trilineata* USNM 64365, USNM 64364 PRI 45417, PRI 68758, UF 45471

Diagnosis: Shell divided by major spiral cords into 3 roughly equal flattened areas.

Description: Protoconch unknown. Turritelliform portion of shell large, 8-12 whorls. Whorl profile subquadrate. 2 strong spiral cords on upper and lower thirds of whorl with a smaller medial cord. D cord present but is the least prominent cord. Numerous fine lineations in addition to the major spiral cords. Turritelliform portion umbilicate. Basal sinus Allmon type 1. Lateral sinus medium depth, uninclined, uninflected, apex medially placed. Aperture rounded square.

Distribution: Latest Miocene? (Matura Fm) – Plio-Pleistocene (Jackson Bluff Fm). Florida. *V. trilineata* Guppy, a potential junior synonym, may be present in the latest Miocene and Pliocene of Trinidad.

Remarks: If better material of *V. trilineata* became available and could be demonstrated to definitively be synonymous with *V. weberi, V. trilineata* would have priority for this species. As lectotype material for *V. trilineata* is in poor condition, however, characters such as growth lines could not be confirmed as definitively synonymous. Should additional better-preserved specimens of *V. trilineata* become *V. trilineata* Guppy 1867 material from Matura, Trinidad is encompassed by *V. weberi*, not *V. woodringi* or *V. spirata*, extending the range for this species to the latest Miocene. Early whorls could easily be mistaken for a normally coiled turritellid. Not known to cement to conspecifics.

Vermicularia woodringi

Synonymy: Vermicularia woodringi Olsson and Harbisson, 1953

Types: Holotype ANSP 19321

Material examined: ANSP 19321, UF 174475, PRI 68757

Diagnosis: V. recta maintains a flattened inner coiling surface as opposed to a rounded one, and is generally larger in diameter at a given length than *V. woodringi*, which frequently co-occurs with *V. recta* and is misidentified as such.

Description: Protoconch 250-350 μm. Turritelliform portion approximately 7 whorls. Whorl profile subquadrate. Vermiform portion often irregularly coiled but ma form tubes in association with conspecifics. Typically has multiple loosely coiled or offset whorls before complete separation. 2 Strong spiral cords straddling the middle of the shell, moving posterior (adapically) as the shell becomes uncoiled, and the D cord strengthens. Medial cord becomes the strongest of the 3. Many fine lineations on the vermiform portion, especially the basal part. Basal sinus Allmon type 2. Lateral sinus deep, opisthocline, single inflection on top, apex on upper third of shell. Aperture rounded-square to circular, becoming more circular in the vermiform portion than the turritelliform portion.

Distribution: Pliocene-Pleistocene. Florida; Caloosahatchee Fm., Bermont Fm., Pinecrest beds of the Tamiami Fm. South Carolina, Bear Bluff Fm. North Carolina, Waccamaw Fm. Reported by Olsson and Harbisson (1953) as potentially occurring in the Late Miocene of Bowden, Jamaica, but we observed no corresponding specimens.

Remarks: Often any substantial mass of intercoiled/cemented *Vermicularia* tubes is assigned to *V. recta*, but *V. woodringi* and *V. spirata* also form such associations.

Chapter 3: Unravelling the evolution of the vermiform gastropod *Vermicularia* (Turritellidae) in an eco-evo-devo framework using isotopic sclerochronology

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Abstract— The uncoiled genus *Vermicularia* represent a dramatic departure from typical coiled turritellid morphology, a morphological change associated with ecological changes as well. While most turritellids are semi-infaunal, *Vermicularia* uncoil, with several species becoming vertically oriented, attaching to other organisms or conspecifics as components of reef faunas. Here we employ isotopic sclerochronology to determine the growth patterns of fossil and Recent species in a recently established phylogenetic framework for this clade. This ontogenetic information allows for study of the specific heterochronic mechanisms involved in the origin of these species' morphologies. By coupling knowledge of the specific heterochronic mechanisms with (palaeo)environmental context, we bridge the gap between selection pressures and changes to ontogeny. Peramorphosis (leading to more vermiform morphology) dominates the history of the group, accomplished through pre-displacement, acceleration, and hypermorphosis, but two lineages appear to have undergone paedomorphosis through progenesis and post-displacement. Selection appears to have dominantly been on morphology rather than reproductive mode – the exception being an isolated population of *V. spirata* which appears to have undergone progenesis due to selection for reproductive mode.

Introduction

Questions surrounding the origins of novel traits (such as uncoiling) that give rise to groups recognized as higher taxa remain among the most intriguing questions in evolutionary biology (Jaecks and Carlson 2001; Wagner 2014; Moczek et al. 2015)**.** Evolutionary developmental biology (evo-devo) seeks insight into evolution through a cross-disciplinary understanding of the mechanisms generating novel forms by integrating information from genetic, developmental, ontogenetic, phylogenetic, and the fossil record (Moczek 2012; Sánchez-Villagra 2012; Moczek et al. 2015; Organ et al. 2015; Diogo 2016; Bardin et al. 2017). Evo-devo perspectives expand our understanding of evolution beyond the effects of selection, sorting, and drift on variation to a better understanding of how those variants arise in the first place (West-Eberhard 1998; Gilbert and Epel 2009; Moczek et al. 2015).

Eco-evo-devo further extends this new synthesis by integrating ecological information to understand the impact of the environment on development, and the ecological selective pressures that may have been involved in favoring and driving to fixation certain variants (Gilbert and Epel 2009; Sánchez-Villagra 2012; Abouheif et al. 2014). Recently evo-devo has been expanding rapidly, however most studies are focused on the genetic and developmental aspects, rather than the phylogenetic context or the integration of developmental information with evolutionary hypotheses (Diogo 2016, 2018). While most evo-devoists are presently focused on linking genetics to development and ontogeny (Diogo 2016), we seek to study post-settlement shell ontogeny to understand the evolution of an apparently novel shell form. Here we document the changes in ontogeny that generated uncoiling in turritellids in a

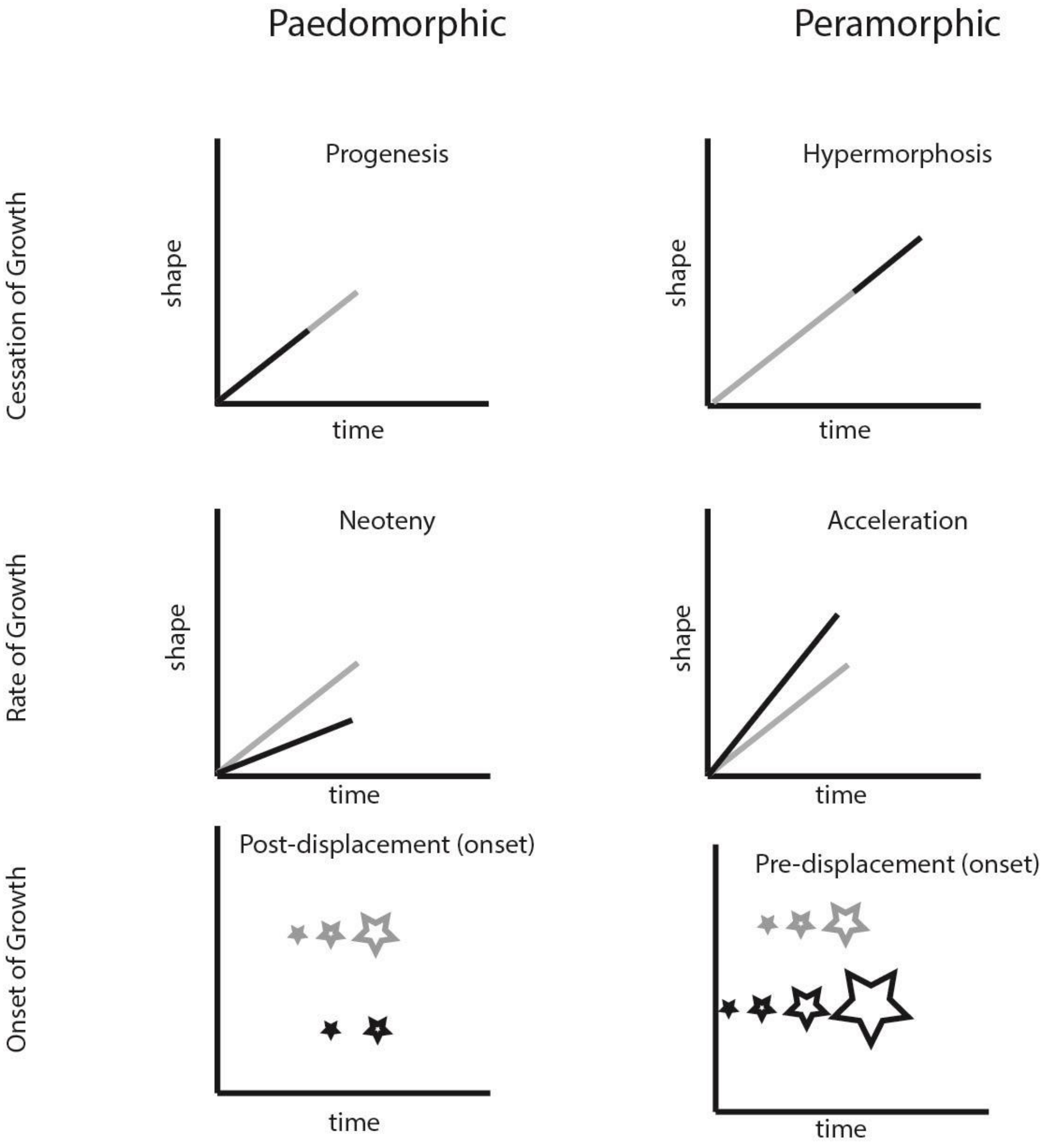

Figure 3.1. Heterochronic processes outlined in Alberch (1979). Ancestral morphology shown in gray, descendant morphology in black.

phylogenetic framework and show how the diversification of this group and the specific changes to ontogeny we observe are linked to environmental changes and the ecology of the taxa. This integration of selection at the ecological level with the mechanisms leading to species-level changes in morphology has been considered both a crucial need of the field of evo-devo (Diogo 2018), and for bridging micro- and macroevolution (Jablonski 2009; Geary et al. 2012) .

Heterochrony

Heterochrony refers to change in the expression or development of a feature (other than scaled size; Shea 1988; Gould 2000a) in a descendant relative to the ancestor at the timepoint used for comparison (De Beer 1930; Gould 1977; Gould 1988). This timepoint may be extrinsic time (Jones 1988; Jones and Gould 1999; Bardin et al. 2017), or more commonly, ontogenetic stage (e.g., reproductive maturity or instar; (De Beer 1930; Gould 1977; McNamara 1983; Landman 1988; 1988a; Jones and Gould 1999; Stephen et al. 2002; McNamara and McKinney 2005). In the most widely employed classification scheme (Jaecks and Carlson 2001), Alberch et al. (1979) outlined six types of heterochronic processes (Figure 3.1). Paedomorphic processes produce juvenilized forms in descendants (or constituent parts under consideration), and peramorphic processes produce descendants that are further along the ontogenetic trajectory than ancestors at a given point (Gould 1977; Alberch et al. 1979; Gould 2000a). Paedomorphic processes include neoteny (slowing of growth), progenesis (early maturity or arresting of morphological development at an earlier stage), and post-displacement of the initiation (relative to cessation) signal for growth such that total time a feature is developing is truncated (Alberch et al. 1979; Smith 2003; McNamara and McKinney 2005). Peramorphic processes include acceleration (faster development), hypermorphosis (prolongation/extention of growth and development), and pre-displacement of the initiation (relative to cessation) signal for growth (such that total growth time is extended) (Alberch et al. 1979; Smith 2003; McNamara and McKinney 2005).

A particular feature may also be displaced relative to other features in an ancestral organism (developing either earlier or later in ontogeny) without the size or shape of that feature being altered (De Beer 1930; Gould 1977; Allmon 1994; Smith 2003; McNamara and McKinney 2005). Parallel language describing ontogenetic stages in the same organism (e.g. larvae to adult, or successive instars) can still be used coherently. The terminology of Alberch et al. (1979), however, can not be used coherently to describe *size* changes of an individual part rather than the overall allometric effect of that size change, or changes in *rate of growth rate change* ('jerk'; the 2nd derivative of velocity in physics) (Gould 2000a). The first because it leads to absurdities (the paedomorphic form of the human head being the result not of neoteny but of hypermorphosis of brain growth; (Shea 1988; Gould 2000a), the latter (*pace* Gould, 2000) not because it is nonsensical, but because the terminology does not exist. The overall shape change can still be described as either acceleration or neoteny, but how that growth rate change was accomplished is not specified in Alberch et al.'s schema (e.g., the descendant may grow 25% more than an ancestor with a steady pace of growth by growing faster the entire time, or if the ancestor's growth rate slows throughout the time period under consideration, the descendant may maintain the initial growth rate). The power of the Alberch et al. (1979) heterochrony model to describe evolutionary change lies in its objectivity and simplicity (Gould 1988; McKinney 1988a), and we do not propose here to complexify the schema.

Understanding the specific mechanisms of heterochrony employed in generating paedomorphic or peramorphic morphology provides insight into the selective pressures that generated heterochronic changes. The immediate adaptive significance of heterochrony is derived either from selection on morphologies themselves, reproductive timing, or both (Gould 1977; McNamara 1988a; Landman and Geyssant 1993; Crampton and Maxwell 2000). Hypotheses related to reproductive strategies have suggested that paedomorphosis by progenesis is linked to an r-selected strategy (earlier reproduction), and is favored in unstable environments, newly colonized regions, in some sexually dimorphic systems where early maturation may be advantageous (e.g. (Neige et al. 1997)), or where resources are abundant with limited predation threat (Gould 1977; Alberch et al. 1979; McKinney 1986; Geary 1988; McNamara 1988a; Landman and Geyssant 1993; Allmon 1994). Hypermorphosis is then associated with increased lifespan, and is related to k-selected strategies, high inter-annual variability in reproductive success (e.g. (Buick and Ivany 2004), and/or stable environments (Gould 1977; McKinney 1986; McNamara 1988a; Landman and Geyssant 1993; Geary et al. 2012).

Paleontological evidence can make important contributions to evo-devo research by providing the only direct evidence of past phenotypic innovations and the order in which they occurred (Raff 2007; Moczek et al. 2015), as well as improving phylogenetic hypotheses (Raff 2007; Organ et al. 2015). To properly test hypotheses for how heterochrony specifically may have shaped evolution in a clade requires:

1) a complete phylogeny (to properly determine ancestor/descendant conditions) (Fink 1982; Geary 1988; Gould 1988; Lindberg 1988; McNamara 1988b; Jaecks

and Carlson 2001; Smith 2003; Organ et al. 2015; Collins et al. 2016; Diogo 2016, 2018)

2) an assessment of whether the change in a particular feature is peramorphic or paedomorphic given the phylogeny (Gould 1977; Alberch et al. 1979; Gould 1988; Gould 2000a; Jaecks and Carlson 2001), and

3) determination of growth rate relative to some size-independent measure of time (Gould 1988; Jones 1988; Shea 1988; Neige et al. 1997).

The measure of time used to determine relative rates may be either extrinsic (real) time (measured in mark-recapture studies of living organisms, or a morphology independent proxy for extrinsic time such as oxygen isotopic sclerochronologies; Jones 1988), a hypothesized morphological proxy of time (“allometric heterochrony”; e.g. decreased spacing between septa in conspecific ammonoids (Landman 1983; McKinney 1988a; Landman and Geyssant 1993; Neige et al. 1997), or an indicator of sexual maturity (Collins et al. 2016). Absolute ages (lifespans and other ontogenetic events) determined based on extrinsic time are the ideal, although they are typically difficult to obtain for fossils or wild- living specimens (Gould 1988; Jones 1988; McKinney 1988a; Bardin et al. 2017), because in the absence of definitive information about time it is difficult to definitively asses heterochronic mechanisms (McNamara 1988b; Allmon 1994; McNamara and McKinney 2005).

The lack of developmental or ontogenetic data has been considered the principal limit to including fossils in evo-devo research (McKinney 1988a; McNamara 1988a; Gould 2000a; Organ et al. 2015). While the earliest stages of embryology are inaccessible in fossil systems (Raff 2007), in organisms with accretionary growth (and minimal skeletal remodeling), such as mollusks, the shell records the entirety of ontogeny, making them excellent subjects for studies of evolution by heterochrony (Geary 1988; Allmon 1994; Neige et al. 1997; Jones and Gould 1999; Crampton and Maxwell 2000; Ivany et al. 2003; Goodwin et al. 2008; Collins et al. 2016). Arthropod instars represent another fruitful means of obtaining fossil ontogenetic information (McNamara 1983; 1988a).

Isotopic sclerochronology (sclerochronology, the molluscan equivalent of dendrochronology; (Jones 1983, 1988; Jones and Allmon 1995; Jones and Gould 1999; Ivany et al. 2003; Goodwin et al. 2008; Ivany 2012) provides a means of determining ontogenetic age data and growth rates, even in fossil organisms, that is independent of size, and derived from the external environment (Williams et al. 1982; Jones 1988; Jones and Gould 1999; Gould 2000a; Schöne et al. 2006; Goodwin et al. 2008; Collins et al. 2016). Seasonal variation in temperature, upwelling, or freshwater input (wet/dry seasonality) can be used to determine ontogenetic age and patterns of growth (Grossman and Ku 1986; Ivany et al. 2003; Buick and Ivany 2004; Schöne et al. 2006; Ivany 2012; Tao et al. 2013; Moss et al. 2016; Anderson et al. 2017). Extrinsic time proxies derived from the environment, (such as cyclical variation in the incorporation of ^{18}O into shell carbonate, or other temperature indicators such as Mg/Ca in a variety of organisms (Jones 1988; Lowenstein and Hönisch 2012; Durham et al. 2017; Saraswat et al. 2017), or Sr/Ca ratio in corals (Saraswat et al. 2017)), are presumably not tightly coupled to morphological evolution (Jones 1988). They are therefore preferable over allometric relationships, and even sexual maturity markers, when assessing heterochronic processes (McNamara and McKinney 2005; Bardin et al. 2017). It is possible, even if unlikely in mollusks, that a species may undergo both progenesis and simultaneously more rapid growth, producing a highly similar form but with additional generations per year, which would only be detectable using proxies related to the external environment.

Despite 30 years of discussion of the technique (Jones 1988), relatively few studies of heterochrony exist in molluscs of any kind integrating isotopic sclerochronologies with phylogenies (Jones and Gould 1999; Goodwin et al. 2008). In studies of heterochrony employing isotopic techniques, bivalves are better represented than gastropods (e.g. (Goodwin et al. 2008), as bivalve shells typically exhibit age-informative growth lines in cross section (Jones et al. 1978; Jones 1988; Jones and Gould 1999; Moss et al. 2016; Moss et al. 2017), while gastropods often do not (Geary 1988; Jones 1988; Allmon 2011). An exception is Geary et al. (2012), who found good correspondence between isotopic data and growth lines in melanopsid gastropods. If shell growth lines can be shown to correspond perfectly or approximately to annual (seasonal) banding in one or a few individuals (Buick and Ivany 2004; Collins et al. 2016), with this data then reasonably extrapolated to many conspecific (or congeneric) individuals (e.g. Collins et al., 2016). It is unfortunate that growth lines do not generally provide reliable age data for gastropods as paleontological, fossil, developmental, and phylogenetic data suggest heterochrony has been important in the evolutionary history of gastropods (Geary 1988; Lindberg 1988; Allmon 1994).

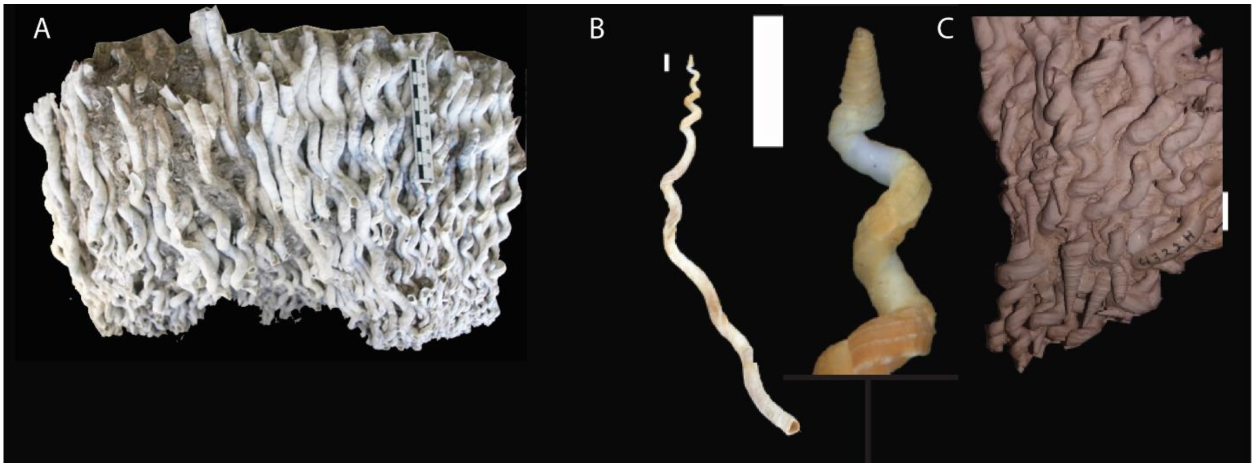

Figure 3.2. Examples of ‘worm-snails’ in the genus *Vermicularia*. A. *Vermicularia recta* B. *Vermicularia spirata* C. *Vermicularia weberi*. White scale bars=1 cm.

Vermicularia

‘Worm-snails’ (Figure 3.2) represent highly derived morphologies, and are therefore are a fascinating evolutionary puzzle – how (and why) does a geometrically regular snail evolve into an irregular winding tube? To be a worm-shaped (“vermiform”) snail is to be an elongated conical tube that does not regularly coil as do most gastropod shells. To elongate the cone while remaining regularly coiled is simply to be a larger snail. To lack (or at some point in ontogeny lose) normal coiling, but remain small, is an interesting innovation, but would never be thought of as ‘worm-like’. This morphology is readily recognized as a different group (and given a genus name) even though species determinations within each group of vermiform snails (the Vermetidae, Siliquariidae and *Vermicularia*; (Bieler 1996)) are difficult. This applies particularly well to *Vermicularia*, which are one of only handful of genera commonly used for the marine family Turritellidae, with most workers referring to most turritellids as belonging to "*Turritella s.l.*" (Allmon 1996; Hendricks et al. 2014).

Vermicularia may be the least (and most recently) derived among the various independent gastropod clades converging on vermiform morphology (including Siliquariidae, and Vermetidae), with an early, coiled portion of the shell clearly demonstrating their turritellid affinity (Anderson et al. 2018). Suture deepening, and occasional uncoiling late in ontogeny or after damage (e.g. failed predation) are known to occur in a variety of turritellids, and these pathologies or "senescence-stage" events show that variation toward vermiform shape exists across the family (Figure 3.3; (Perez 1929; Andrews 1974; Allmon 2011)). This variation may have become fixed in *Vermicularia,* (McKinney 1988b; Moczek 2012). *Vermicularia* is also an ideal taxon for considering heterochronic processes because the clade to which it belongs, Turritellidae, has been the subject of numerous isotopic analyses for the purpose of paleoclimate reconstruction (Jones and Allmon 1995; Andreasson and Schmitz 1996; Andreasson and Schmitz 2000; Latal et al. 2006; Allmon 2011; Baltzer et al. 2015). These paleotemperature/seasonality estimates can be interpreted in terms of periodicities, particularly, annual climatic variability, and thus provide lifespan information when entire shells have been sampled at sufficient resolution (Jones 1983, 1988; Jones and Allmon 1995; Jones and Gould 1999; Ivany et al. 2003; Goodwin et al. 2008; Ivany 2012).

Here we show how such drastic morphological changes were generated using relatively simple changes in timing of ontogenetic events (heterochrony), and tie these proximate causes of form to the ecological (selective) pressures which ultimately led to the diversification of this group over the last 8 million years. When considering peramorphosis as opposed to paedomorphosis in *Vermicularia*, the juvenile form is for more of the shell to be turritelliform (regularly coiled) while the late ontogenetic form is more vermiform, which generally aligns alterations of growth with alterations of form, however it is the *overall shape* (form), that is under consideration when determining heterochronic processes involved, not size. We also establish how these reef-forming snails have evolved in an eco-evo-devo (Gilbert and Epel 2009; Abouheif et al. 2014)framework which would satisfy Waddington's quest for "the whole real guts of evolution" (Waddington, 1967 quoted in Gould, 2002, p. 719), linking the ultimate causes (specific selection pressures; Geary 1988; Jones 1988) to the resultant forms by

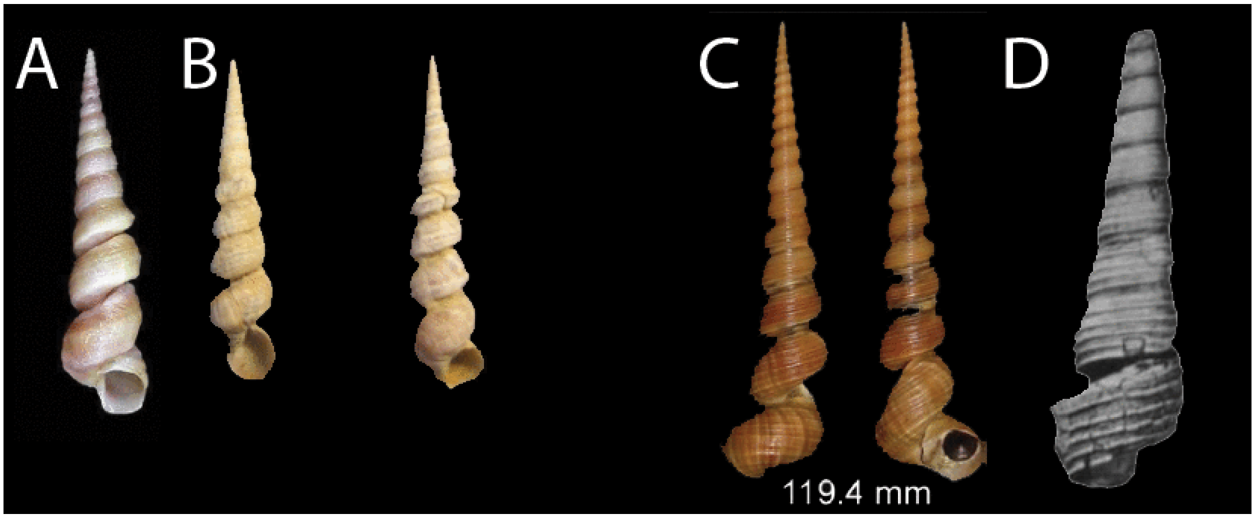

Figure 3.3 Non-*Vermicularia* turritellid individuals exhibiting aberrant uncoiled morphologies. A. and B. *Turritella communis* C. *Turritella terebra* D. *Turritella vertebroides* (Modified from Sohl, 1964)

understanding what specific, proximate, changes to growth and development evolved in each lineage to generate their observed morphologies (Amundson 2005; Gilbert and Epel 2009; Organ et al. 2015; Diogo 2016).

We have compiled lifespan estimates from the literature for 21 species from non-*Vermicularia* turritellids (Table 3.1) generated as a byproduct of paleoclimate and natural history research. Turritellids are nearly uniformly short lived (mean lifespan 2.4 years, median lifespan 2 years), and species which live longer than 1.5 years typically show a period of rapid growth in the first year followed by a pronounced decline in growth rate (Allmon, 2011). It is likely that this decline in growth rate in most species corresponds to an allocation of resources towards reproduction ((Allmon 2011)— a pattern observed in other gastropods with rapid juvenile growth rates (Cudney-Bueno et al. 2008) – and indicating maturity at 1 year is typical for turritellids. Growth rates for conspecifics may vary among locations (Allmon et al., 1994; Scott, 1997; Bax et al., 2003; Allmon, 2011), possibly due to variation in plankton availability (Allmon et al., 1994; Teusch et al., 2002; Allmon, 2011).

Figure 3.4. *Turritella altilira.* Arrow indicates a substantial increase in suture depth (potentially homologous to the earliest stage of uncoiling) late in ontogeny (last 2-3 whorls, after approximately 1 year of growth; Anderson et al., 2017).

As the outgroup comparison for evolutionary hypotheses we chose *Turritella* (*Torcula*) *altilira* (Conrad; Figure 3.4). Like most *Vermicularia, T. altilira* inhabited shallow (<100 m; typically, ~60 m) tropical waters (Hendy, 2013; Anderson et al., 2017; 2018), and they have been assigned to the genus *Torcula*, which is recovered as the sister taxon to *Vermicularia* in molecular analyses (Anderson et al. 2018). Additionally, while most isotopic studies generated for the purposes of paleoenvironmental reconstruction do not extensively sample more than 2 conspecifics from a particular locality (due to the expense involved in high-resolution sampling), Anderson et al. (2017) sampled 10 individuals of *T. altilira* from the Miocene Gatun Formation (Panama) in order to assess variation in upwelling intensity (and associated marine nutrient supply). *T. altilira,* like many turritellid species (Allmon, 2011), also exhibits a pronounced increase in suture depth (relaxing of contact between whorls; Figure 3.4) late in ontogeny (after reaching approximately 1 year in age). This deepening of the suture is homologous to the earliest stage of open coiling (separation of whorls).

Table 3.1. Lifespan determinations for non-*Vermicularia* turritellid species based on isotopic sclerochronologies. Species with lifespans greater than 3 years are in bold.

Species	**Lifespan**	**Citation**
Colposigma capitanea	3	Khan et al., 2017
Maoricolpus roseus	3	Allmon et al. 1992
Mesalia claibornensis	1.5	Andreasson and Schmitz 2000
Torquesia sulcifera	**4**	**Huyghe et al. 2015**
Turritella abrupta (robusta)	2-3 (+?)	Anderson and Allmon 2017
Turritella altilira	3	Anderson et al. 2017
Turritella apicalis	1.5	Jones and Allmon 1995
Turritella bacillum	2	New data (Kelley, p.c. 2014)
Turritella banksi	1	New data (Sang, p.c. 2014)
Turritella cingulate	2	Teusch et al. 2002
Turritella cingulatiformis	3	Teusch et al. 2002
Turritella communis	**5**	Baltzer et al. 2015
Turritella dobyensis	1.5	Andreasson and Schmitz 2000
Turritella duplicate	3	Waite and Allmon 2013
Turritella duplinensis	2.5	Allmon, 2011
Turritella eryna	1-1.5	Latal et al., 2006
Turritella gladeensis	1	Jones and Allmon 1995
Turritella gonostoma	1.5	Allmon et al., 1992
Turritella imbricataria	3	Andreasson and Schmitz 1996
Turritella leucostoma	2	Waite and Allmon 2013
Turritella nasuta	1.5	Andreasson and Schmitz 2000
Turritella terebra	2-2.5	New data

Materials and Methods

Materials

Specimens were obtained for isotopic analysis from the Museum of Comparative Zoology (Harvard University, Cambridge, MA, USA), the Paleontological Research Institution (Ithaca, NY, USA), and the Florida Museum of Natural History (University of Florida, Gainesville, FL; Table 3.2). Additionally, specimens of a population of *V. spirata* which retain coiled morphology throughout ontogeny (Gould, 1968; 1969; ch 2) were collected from Walsingham Pond, Bermuda for isotopic analysis. Two specimens from this population were examined, one which uncoils, and one which does not, despite being the largest collected individual (of several hundred examined). As the goal of isotopic sampling was determination of lifespan and growth rate individual specimens exemplifying typical to large sizes were chosen for sampling. As isotopic sampling is a destructive technique, resulting in a series of scratches made to the specimen, and high-resolution data is expensive to obtain, we opted for increased taxonomic coverage of Western Atlantic species rather than resampling of conspecifics. *V. bathyalis* Petuch 2002, *V. frisbeyae* McLean 1970, *V. gracile* Maltzan 1883*,* and *V. katiae* Anderson et al. 2018 were not sampled as an extremely limited number of specimens of these species are presently available in museum collections. Conspecific turritellids typically do not vary greatly in growth rate under the same environmental conditions, and the largest dataset of conspecifics from the same locality (Anderson et al., 2017) indicates that first year growth in various *T. altilira* individuals remained within 10% of mean growth for the species.

Isotopic sclerochronology

Specimens were washed, cleansed ultrasonically for 5-10 min, and serially sampled using a dental drill for combined ^{13}C and ^{18}O isotopic sclerochronologies. Specimens were sampled at high resolution (close sample spacing) to assure clarity of seasonal signal and relative growth rates. Analysis of oxygen and carbon stable isotopes was performed at the University of Florida (*V. fargoi, V. spirata* (MCZ specimen), *V. weberi, V. woodringi*), the University of Michigan (*V. recta, V. spirata* from Walsingham Pond), and the University of Kansas (*V. lumbricalis*). Samples from each shell were analyzed at a single lab. A Finnigan-MAT 252 with Kiel III carbonate preparation device was used at the University of Florida. A Finnigan MAT-251 with Kiel carbonate preparation device was used at the University of Michigan. A Finnigan MAT 253 with a Kiel III carbonate preparation device was used at the University of Kansas. All values are reported relative to a Vienna Pee-Dee Belemnite (VPDB) standard. Notation was made regarding which samples bounded the

Table 3.2. *Vermicularia* specimens used in isotopic analyses. UF University of Florida Museum of Natural History; MCZ Museum of Comparative Zoology, PRI Paleontological Research Institution.

Species	Authority	Specimen ID
V. fargoi fargoi	Olsson 1951	UF 277956
V. lumbricalis	Linnaeus 1758	PRI 73787
V. recta	Olsson and Harbisson 1953	PRI 76998
V. spirata spirata	Philippi 1836	MCZ 382941
V. weberi	Olsson and Harbisson 1953	PRI 45417
V. woodringi	Olsson and Harbisson 1953	PRI 68757
V. spirata (Walsingham Pond)	Philippi 1836	Anderson personal collection

initiation of uncoiling. Spiral distance to each sample was measured along the outside of the shell using string to provide the most accurate comparison of growth among these irregular forms.

Quantification of growth data

Spiral growth was measured rather than linear growth as it is a more appropriate measure of growth in irregularly growing gastropods such as *Vermicularia*. After sampling a string was wrapped along the lateral portion of the shell, marked at locations corresponding to samples, and measured using an electronic caliper. Spiral distances between annual peaks were used to characterize growth rates. Uncoiling timing was characterized as 1 year if it took place approximately when the seasonal sine curve returned to the antinode matching original polarity, ½ year if it was in the opposite seasonality, and ¼ year if it took place significantly before reaching the antinode in the opposite seasonality.

Interpretation of heterochrony

We use the phylogeny of Anderson et al. (2018) to infer relationships (Figure 3.5). While heterochronic changes can be directly documented in anagenetically evolving lineages (Jaecks and Carlson 2001), cladogenetic lineages require hypotheses to be made regarding ancestral state. We chose to use the most parsimonious hypothesized ancestral state (minimizing transitions) when making heterochronic hypotheses in lineages evolving by cladogenesis, treating the heterochronic change as an autapomorphy or synapomorphy.

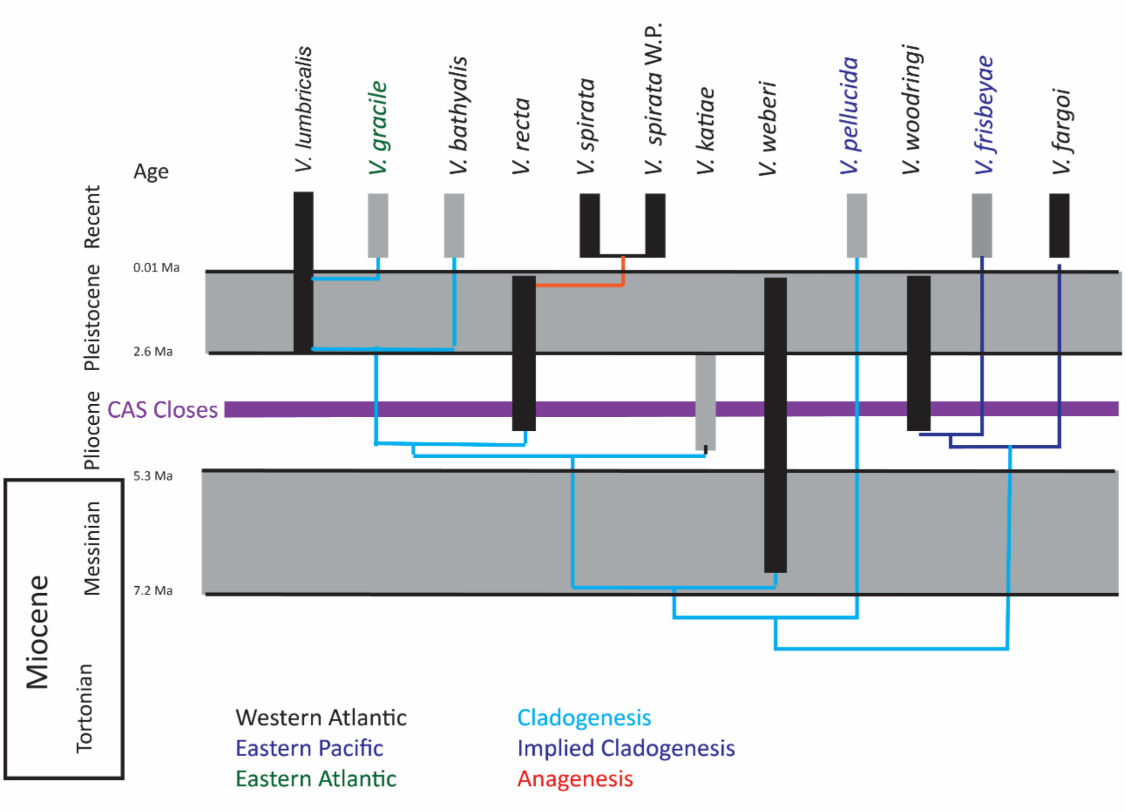

Figure 3.5. Phylogeny of *Vermicularia* species (modified from Anderson et al. 2018). Species for which isotopic sampling was completed shown in black, species which were not sampled in grey.

Results

Isotopic sclerochronologies for *V. fargoi, V. lumbricalis, V. recta, V. spirata, V. weberi, and V. woodringi* (Figures 3.6-11) indicate that the age at which uncoiling began ranged from approximately ¼ year (in *V. lumbricalis* and *V. spirata*) to 1 year (*V. weberi*) (Table 3.3). Lifespans observed ranged from 1 to 5 years (Table 3.4). Of species which lived longer than 1 year, 3 had second year growth rates which were at least 75% of the first year of growth (*V. recta, V. spirata*, and *V. fargoi*) (Table 3.4). The longest living species *V. recta* and *V. spirata* had growth rates that did not differ substantially among years 1-4*. V. recta* may exhibit a decline in growth rate during year 5. The specimen of *V. spirata* sampled had multiple break-repair scars during year 4 of growth, and thus this measure likely underestimates actual growth during this year. Specimens of *V. spirata* from Walsingham Pond are substantially smaller, and isotopic sclerochronologies (Figure 3.12) indicate that they live approximately 1-1.5 years. Most of V. spirata from this locality do not uncoil, but one specimen which does uncoils just prior to 1 year (Figure 3.12a).

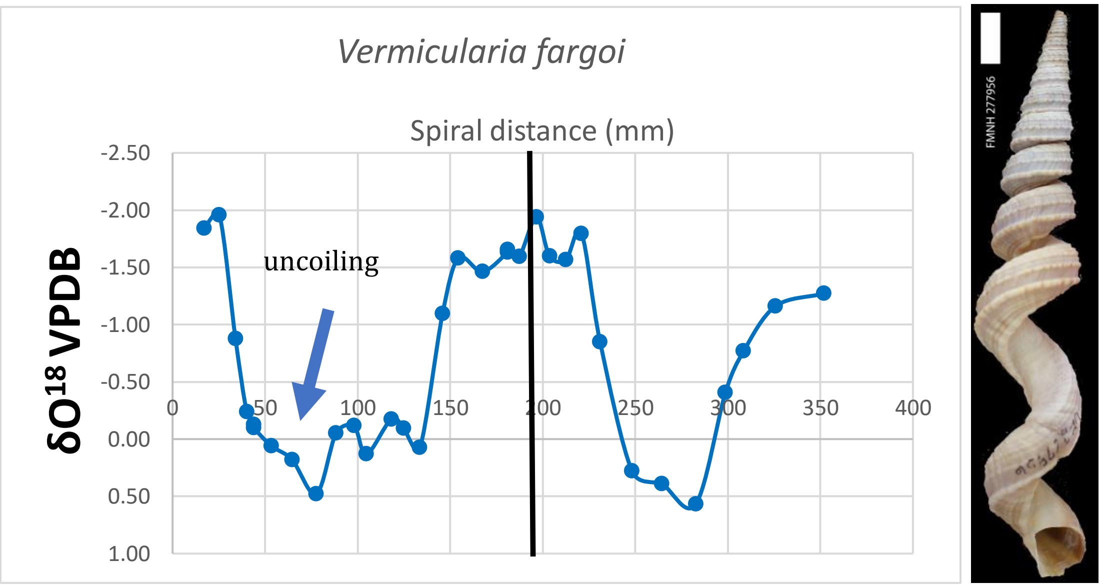

Figure 3.6. Isotopic sclerochronology of Recent *Vermicularia fargoi* UF 277956. Point of uncoiling indicated with the arrow. Black bar indicates completed year.

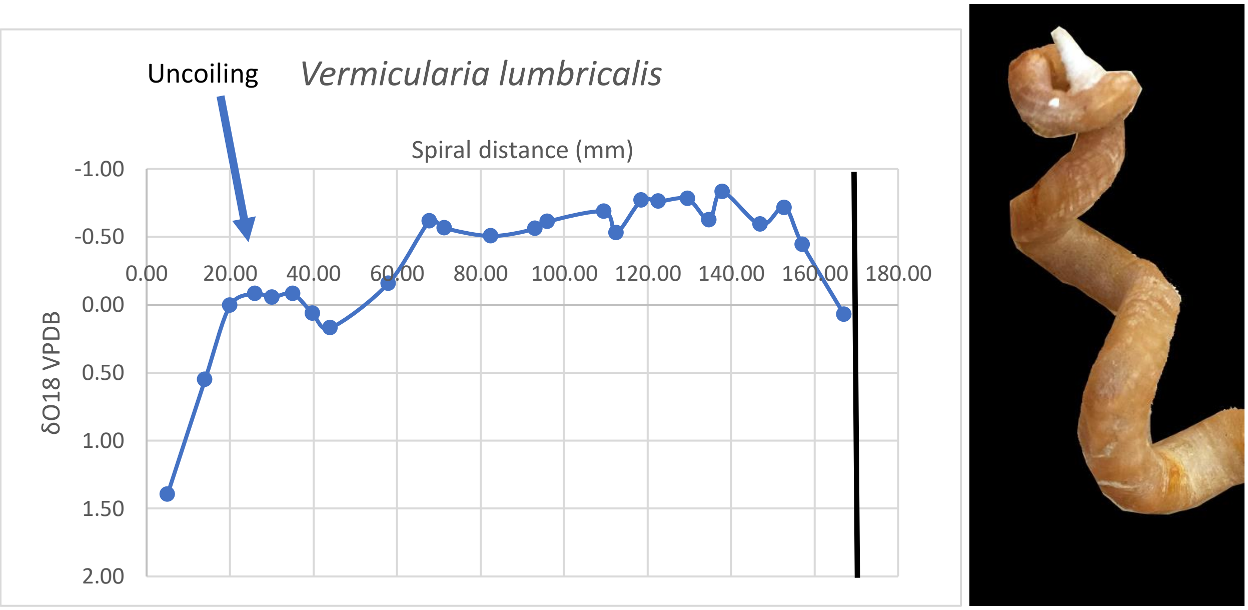

Figure 3.7. Isotopic sclerochronology of Recent *Vermicularia lumbricalis* (=*knorrii*) PRI 73787. Point of uncoiling indicated with the arrow. Black bar indicates completed year.

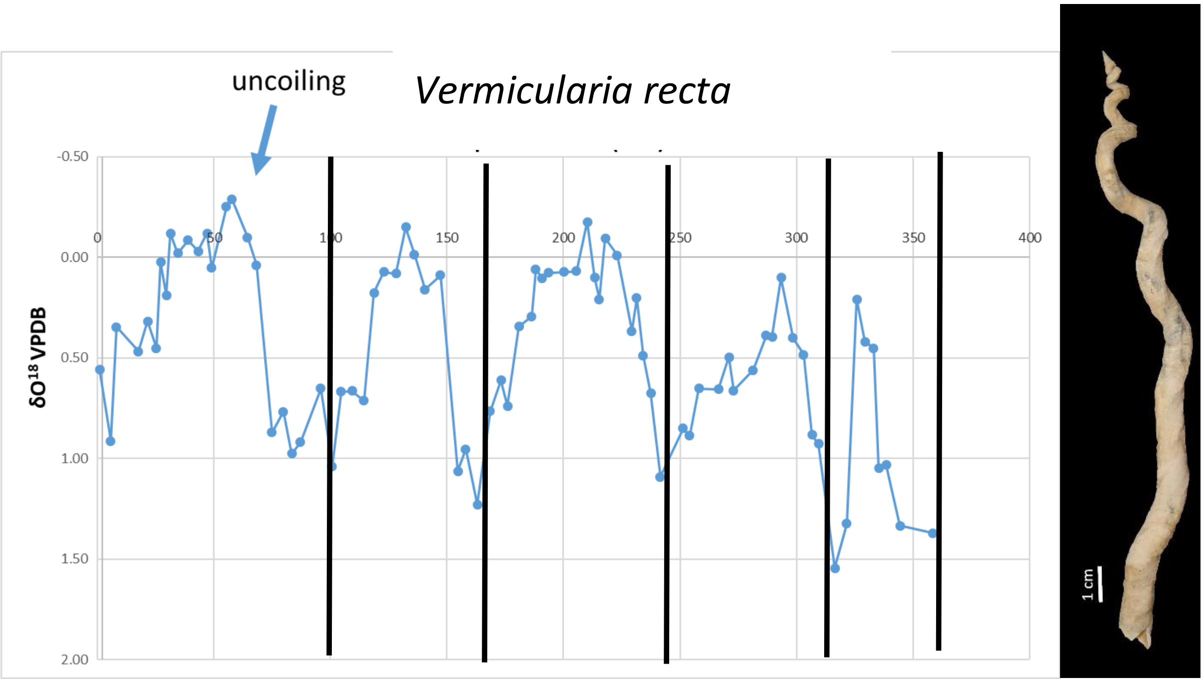

Figure 3.8 Isotopic sclerochronology of Plio-Pleistocene *Vermicularia recta* PRI 76998. Point of uncoiling indicated with the arrow. Black bar indicates completed year.

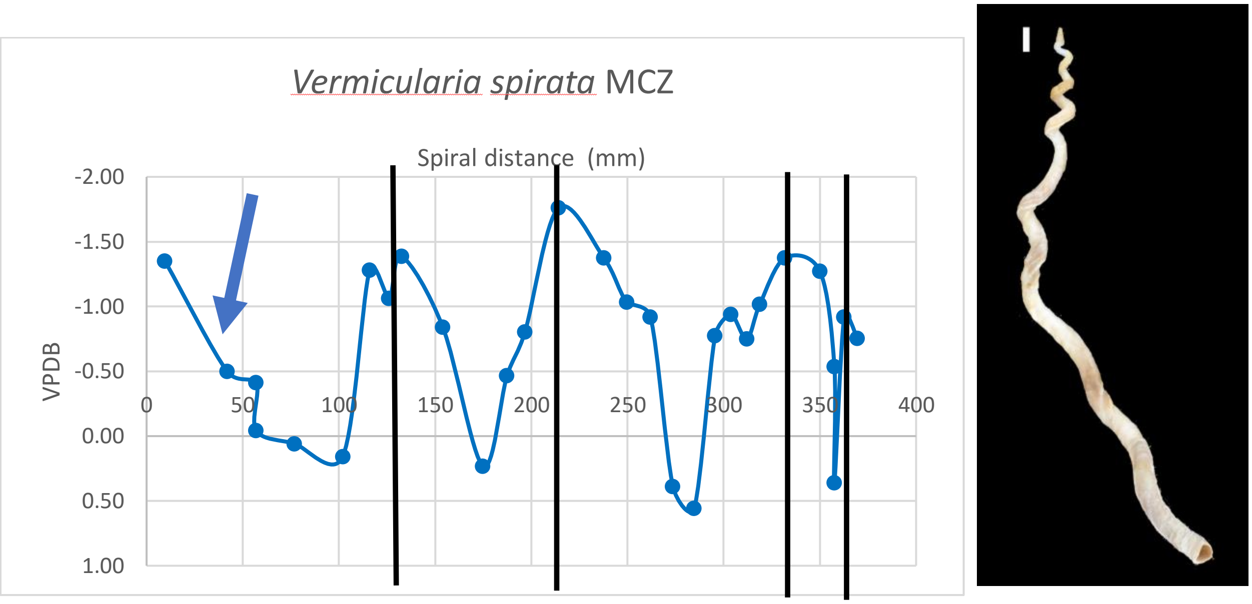

Figure 3.9 Isotopic sclerochronology of Recent *Vermicularia spirata* MCZ 382941. Point of uncoiling indicated with the arrow. Black bar indicates completed year.

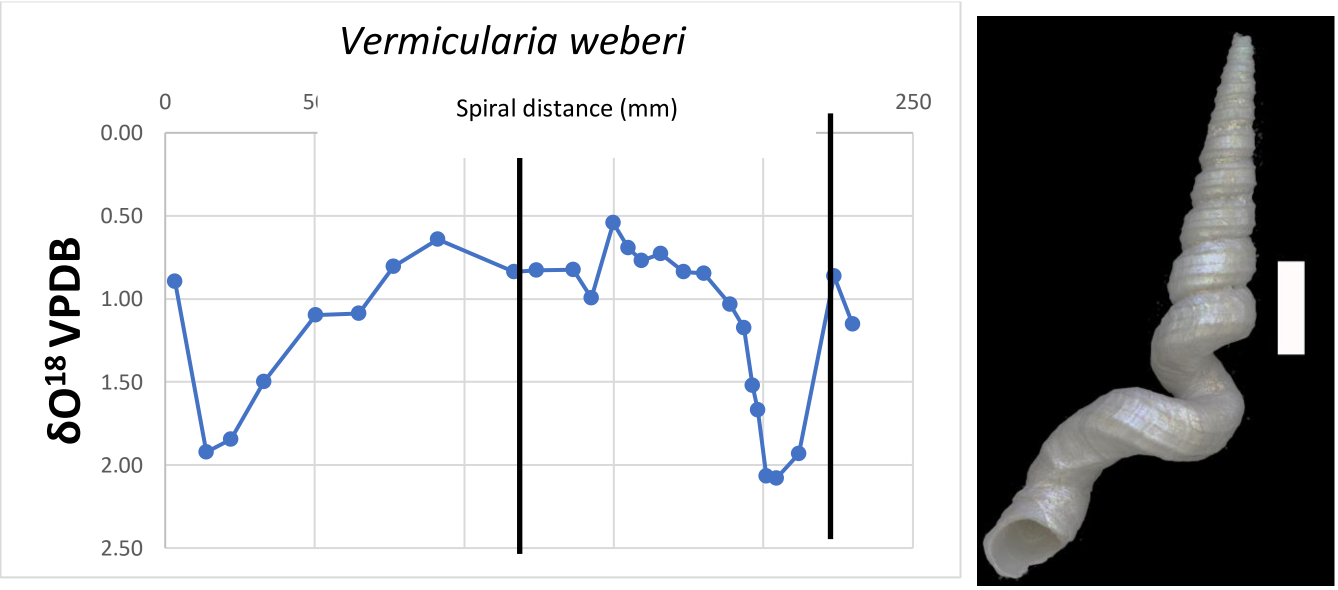

Figure 3.10 Isotopic sclerochronology of Plio-Pleistocene *Vermicularia weberi* PRI 45417. Point of uncoiling indicated with the arrow. Black bar indicates completed year.

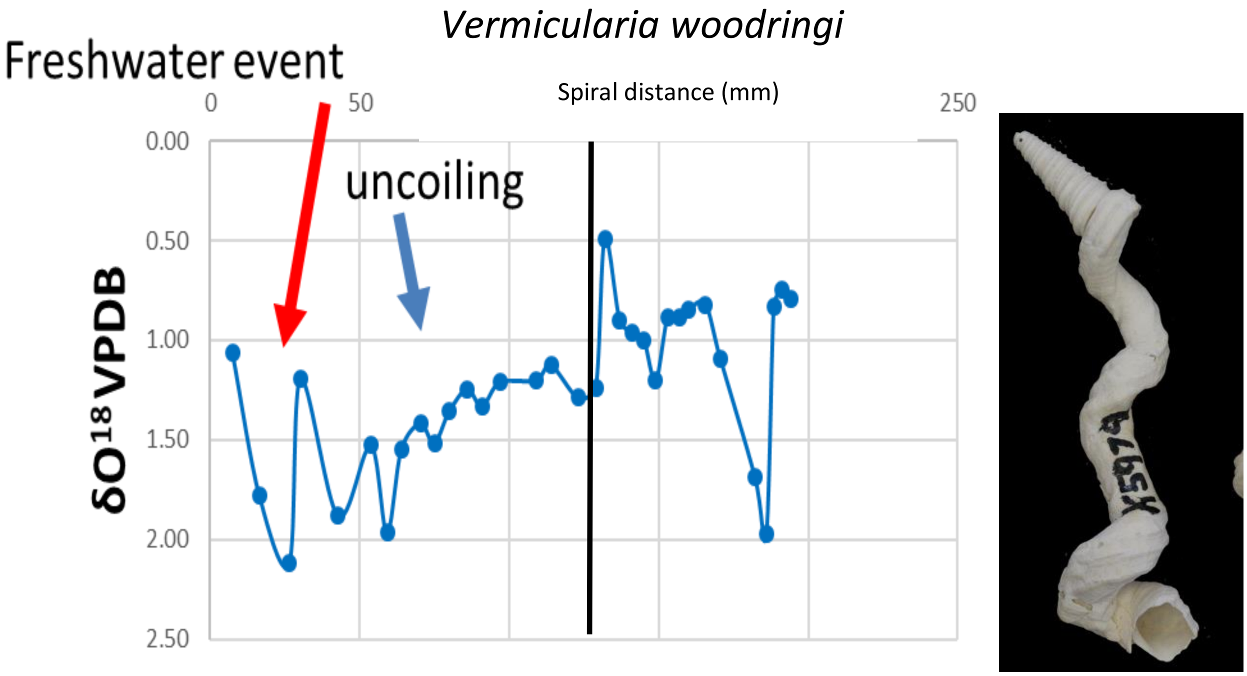

Figure 3.11. Isotopic sclerochronology of Plio-Pleistocene *Vermicularia woodringi* PRI 68757. Point of uncoiling indicated with the blue arrow. Black bar indicates completed year. The early excursion indicated by the red arrow is likely due to a sudden influx of freshwater (as indicated by carbon isotopes; (Jones and Allmon 1995; Tao et al. 2013)) and not an annual cycle of extremely limited growth.

Table 3.3 Inferred ages and spiral growth distances for the onset of open coiling.

Species	Inferred age of onset of open coiling	Spiral Distance (mm)
T. altilira	Loosens ~1 year, never fully uncoils	181
V. fargoi fargoi	0.5 years	80
V. lumbricalis	0.25	18
V. recta	0.5 years	64
V. spirata spirata	0.25 years	15
V. weberi	1 year	149
V. woodringi	0.5 years	120
V. spirata (Walsingham Pond)	Most never (>1.5 years); 1 ~0.75 year	58 mm

Table 3.4. Lifespan and annual growth estimated from isotopic sclerochronologies. Multiple break/repair scars were present in year 4 of V. spirata's growth which may have caused it to be unusually short.

Species	Lifespan	Growth Year 1 (mm)	Growth Year 2	Growth Year 3	Growth Year 4	Growth Year 5	2nd year growth as % of first year's growth	Total growth by year 2 (mm)	Total growth (mm)
T. altilira	3	212	113	N/A	N/A	N/A	53%	325	325
V. fargoi fargoi	2	196	156	N/A	N/A	N/A	80%	352	352
V. lumbricalis	1	167	N/A	N/A	N/A	N/A	N/A	167	167
V. recta	5	84	79	78	75	42	94%	163	358
V. spirata spirata	4	116	98	117	38*	N/A	84%	214	369
V. weberi	2	136	87	N/A	N/A	N/A	64%	223	223
V. woodringi	2	124	80	N/A	N/A	N/A	64%	204	204
V. spirata (Walsingham Pond)	1.5	75	N/A	N/A	N/A	N/A	N/A	N/A	75

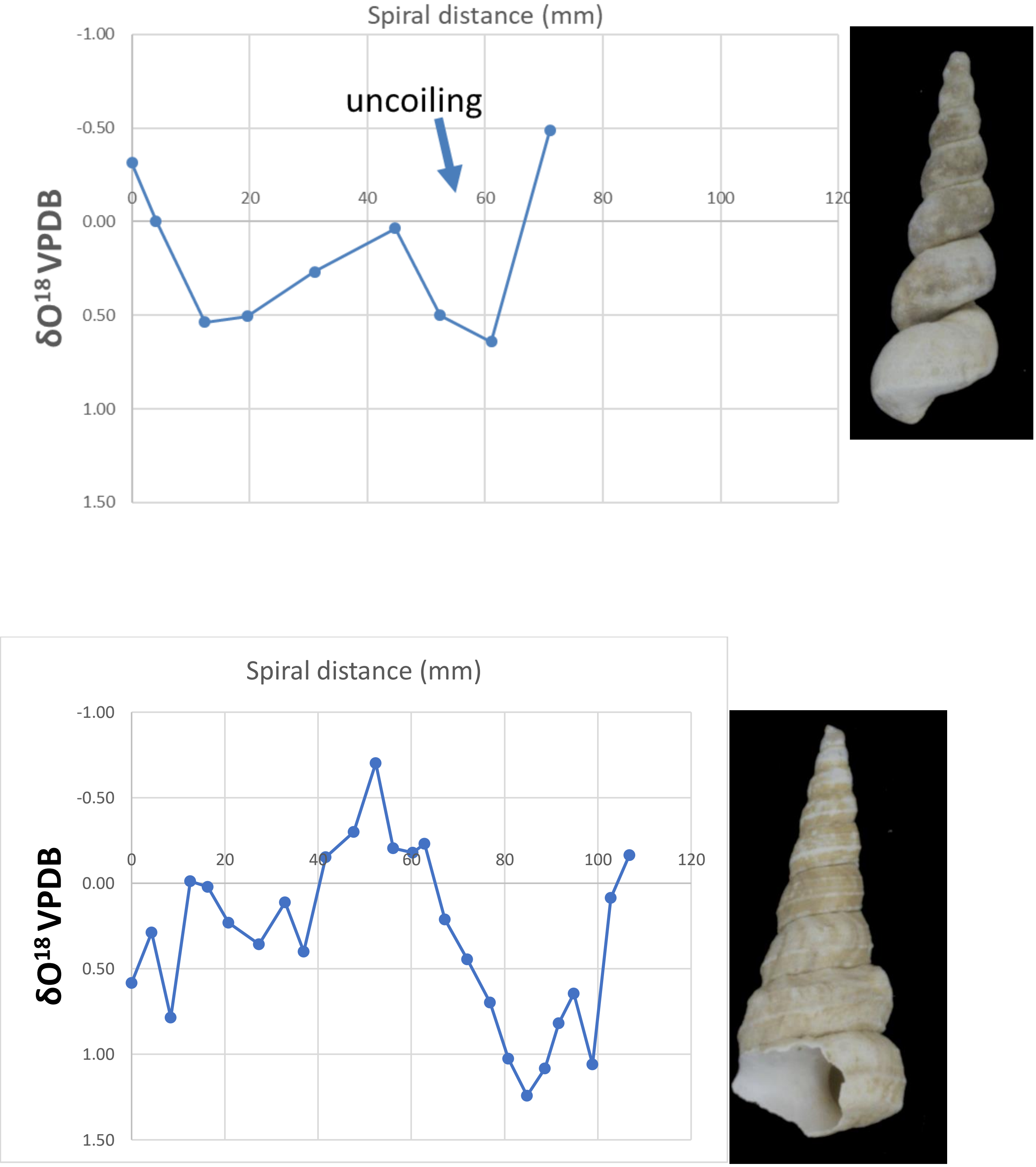

Figure 3.12. Isotopic sclerochronologies of *Vermicularia spirata* from Walsingham Pond (Bermuda) which do (A) and do not (B) uncoil. Anderson personal collection.

Discussion

Heterochronic processes observed

Integrating the information obtained from isotopic sclerochronology with the phylogeny of Anderson et al. (2018) demonstrates the importance of heterochronic processes in the evolution of *Vermicularia* (Figure 3.13). Peramorphosis occurs through pre-displacement, acceleration, and hypermorphosis, and paedomorphosis occurs through progenesis and post-displacement.

The most parsimonious interpretation for uncoiling is that *Vermicularia* is characterized by a pre-displacement of uncoiling to approximately 0.5 years, with V. weberi reversing this trend and post-displacing uncoiling to 1 year in age. It is only slightly less parsimonious to consider uncoiling at one year to be primitive for the *Vermicularia* and for the *V. woodringi* + *V. fargoi* and *V. lumbricalis* + *V. spirata* lineages evolve earlier uncoiling through parallelism. *V. lumbricalis* and *V. spirata* also each exhibit further pre-displacement of uncoiling to noticeably earlier than ½ year, which arose independently in each lineage as *V. recta* (the phylogenetically inferred ancestor of *V. spirata*) uncoiled at approximately ½ year. The Walsingham Pond *V. spirata* population in turn lost uncoiling by post-displacement of uncoiling (unless in the presence of *Oculina*; (Gould 1969), as indicated by the late occurrence of uncoiling in specimens which do uncoil.

Modifications to the relative size of the uncoiled portion, other than altering the timing of uncoiling, also occur throughout the phylogeny. Hypermorphosis occurs in the *V. recta—V. spirata* lineage, with nearly double the inferred ancestral lifespan (2 years for *V. weberi*, and *V. woodringi* + *V. fargoi*). A lifespan of 5 years, while long for turritellids, is not excessive for gastropods in general. For example, the modern tropical American muricid *Hexaplex nigritus* lives at least 8 years (Cudney-Bueno et al. 2008), and *Conus* species may live longer than 20 years ((Kohn and Perron 1994; Kobash and Grossman 2003; Gentry et al. 2008; Graniero et al. 2017). Progenesis occurred in the Walsingham Pond population of *V. spirata*, which does not appear to live longer than 1.5 years (based on the largest specimen recovered). Acceleration took place in *V. fargoi, V. lumbricalis*, and *V. recta—V.spirata*. Acceleration likely arose independently in each lineage, with both *V. fargoi* and *V. recta—V. spirata* maintaining growth rates similar to juvenile growth rates in later years, and *V. lumbricalis* experiencing an increase in the rate of growth during the first year. Progenesis only occurs once on the tree; in the Walsingham Pond population of *V. spirata*.

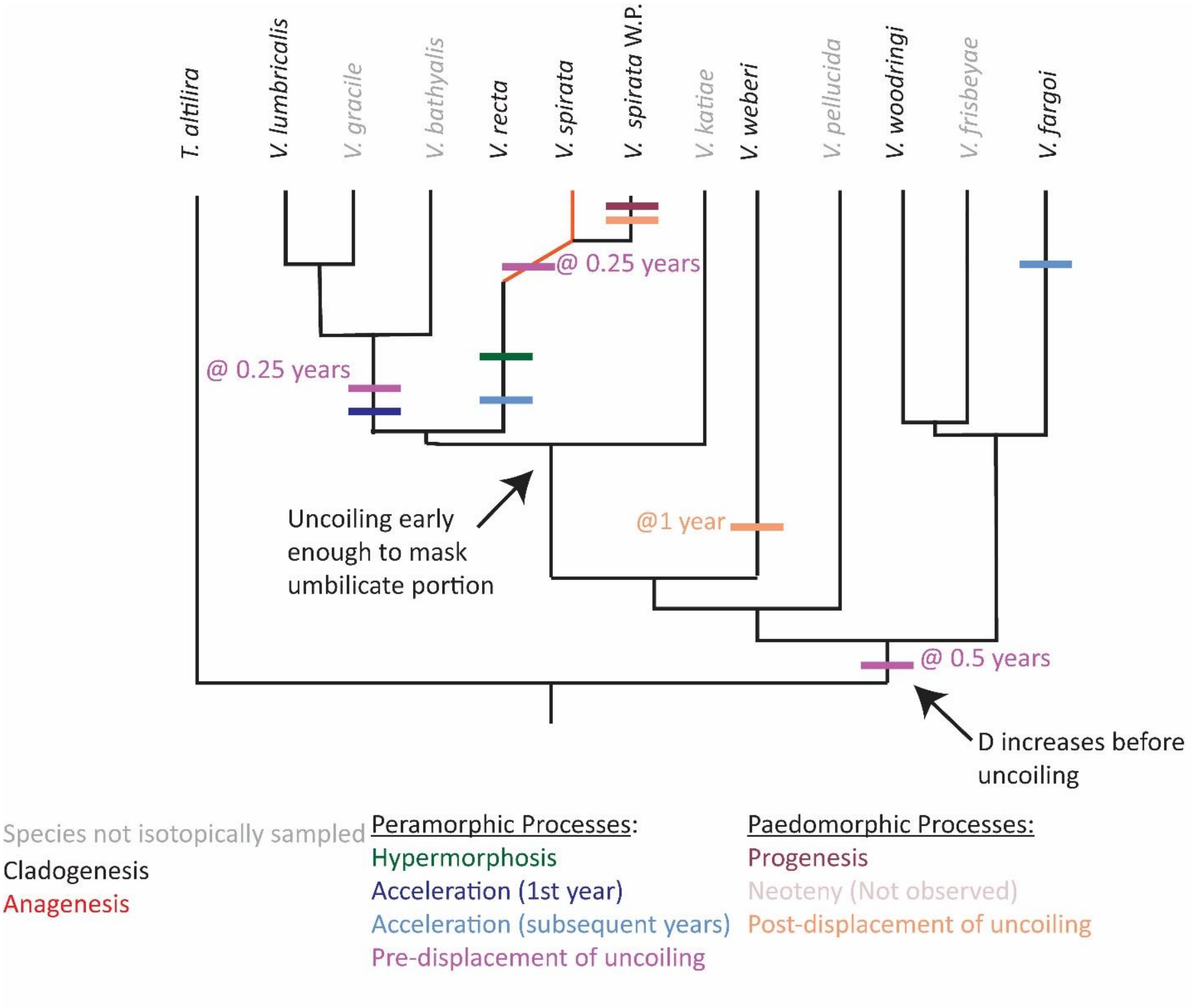

Figure 3.13. Heterochronic changes affecting the evolution of vermiform morphology in *Vermicularia*. Branch lengths within *Vermicularia* clade indicative of stratigraphic timing of branching minimizing ghost ranges (see Anderson et al., 2018), except for the outgroup (*T. altilira*) which diverged from the *Vermicularia* lineage at least by the Miocene.

Ecological Changes and Selective Pressures

By uniting knowledge of the timing of specific heterochronic mechanisms employed with paleoenvironmental context and natural history information derived from Recent *Vermicularia* we can determine what selective factors were important in these transitions. Uncoiling in *Vermicularia* facilitates attachment and, in some species, alters the growth trajectory. Coiled morphology, in contrast, facilitates mobility and burrowing, provides protection against predation, or may occur as a heterochronic by-product of selection for earlier reproduction. Potential selective reasons for elongated (vermiform) morphology in *Vermicularia* include facilitating more rapid upward growth (access to food), adaptation to soft substrate, or as a heterochronic by-product of selection for increased lifespan (selection for multiple reproductive seasons). If multiple peramorphic or paedomorphic processes take place it suggests that selection is for the morphology rather than reproductive mode. If only progenesis or hypermorphosis are observed, this suggests that selection on reproductive mode may be sufficient. If the environmental conditions also suggest selection on either morphology or reproductive mode are likely then we may confidently infer the historical selective regime.

During the late Pliocene the environment of the Western Atlantic was drastically altered by the restriction and subsequent closure of the Central American Seaway 3.5-2.7 Ma (Molnar 2008; (Cronin and Dowsett 1996; O'Dea et al. 2007; 2016; 2018). Productivity was dramatically reduced ((Allmon 1992b; Allmon et al. 1996; Collins 1996; Allmon 2001; Todd et al. 2002; O'Dea et al. 2007; O'Dea and Collins 2013) due to the loss of communication of upwelling Eastern Pacific waters (O'Dea et al. 2007; Jackson and O'Dea 2013; Anderson et al. 2017), changes in circulation which may have reduced local upwelling (Hayes 1989; Maier-Reimer et al. 1990; Allmon et al. 1996; Cronin and Dowsett 1996; O'Dea et al. 2007; Leigh et al. 2014), and possibly decreased riverine nutrient input from the western Amazon-Orinoco paleofluvial system which ceased to be connected to the Caribbean coast 3.2—1.7 Ma ((Aguilera et al. 2013); Sang et al. 2018). This change in nutrient regime resulted in substantial extinctions of predatory and suspension feeding taxa (Allmon 2001; Todd et al. 2002; O'Dea et al. 2007; Smith and Jackson 2009)), including turritellids. Apart from occasional *Vermicularia* dominated reefs (*e.g.* the Pinecrest "*Vermicularia* beds" in Florida (Allmon 1993), and reef communities of the Carolinas (Pearse and Williams 1951)), abundant turritellid assemblages/communities only occur in regions of localized upwelling (Petuch 1976; Todd et al. 2002). These changes did, however, favor the expansion of corals (Highsmith 1980; Birkeland 1987; Collins 1996; Todd et al. 2002; Leigh et al. 2014; Klaus et al. 2017). While other turritellids declined, *Vermicularia* diversified, such that the majority of modern western Atlantic turritellids (4 of 7) are now *Vermicularia* ((Allmon 1992b, 2001)Anderson et al. 2018).

Most *Vermicularia* cement to hard substrates (Anderson et al. 2018), which expanded in the Western Atlantic after the closure of the seaway (Glynn 1982; Cortés 1993; Lessios 2008; Leigh et al. 2014), while most other turritellids are semi-infaunal (Allmon 1988; 2011). In fact cementing 'worm-snails' (Vermetids, Siliquariids, and *Vermicularia*) generally increase in abundance as corals, rubble, and sponge substrates increase on the sea floor (Todd et al. 2002). We propose that this defensive strategy, and subsequent inhabitation of coral and sponge hosts, released them from predatory selection against uncoiled morphology and facilitated their subsequent evolution into members of reef communities, or reef formers themselves ((Pearse and Williams 1951)).

As reef-associated suspension feeders *Vermicularia* would have been under selection for rapid upward growth (Gould 1969) to feed. Any heterochronic changes that increased the size of late-ontogenetic vermiform, tubelike portion of the shell would therefore be selected, favoring peramorphic forms. Earlier deflection of the coiling axis, if a suitable safe host is found, is perhaps the most efficient means, as acceleration in shell growth likely has energetic consequences for reproductive effort (Palmer 1983). Acceleration in the *V. lumbricalis* (=*knorrii*) lineage takes place by increasing the growth during the first year, while the anagenetic *V. recta*—*V. spirata* lineage and *V. fargoi* lineages accelerate growth by maintaining 80% or more of the rapid 1st year growth rate in the second year, while most turritellid growth rates precipitously decline (following Gould, 2000, it would be inappropriate to consider this a form of post-displacement, although the underlying genetic mechanism may be the delay in the signal to slow down growth, or maintenance of the signal maintaining the initial growth rate). The *V. recta*—*V. spirata* lineage, which may form reefs entirely with conspecifics and typically inhabits the most stable environment succeeds in the hat trick becoming hypermorphic, with approximately double the lifespan of most turritellids. The combination of acceleration and hypermorphosis suggests that it is in fact the elongated morphology which is under selection, rather than reproductive strategy exclusively, as acceleration is thought to be favored as part of r-selected strategies, while hypermorphosis is associated with K-selected strategies (McKinney and McNamara 1991; Allmon 1994). The combined effect of all peramorphic types of heterochrony (McNamara and McKinney 2005) in the

V. recta—V. spirata produces the extreme disparity between these species and regularly coiled turritellids. *V. fargoi* does not adopt a vertical orientation, and peramorphic expansion of the vermiform portion in this taxon may be related to its soft-substrate habitat; (Olsson 1951; Yochelson 1971; Gubanov et al. 1995; Petuch and Myers 2014) Anderson et al. 2018).

We identify two paedomorphic lineages: *V. weberi* and the Walsingham Pond population of *V. spirata*. *V. weberi* co-occurs with *V. recta* and *V. woodringi*, both reef-forming lineages, and may have evolved towards more typical turritellid morphology by post-displacement of uncoiling if the reef niche space was filled. Alternatively, it is only slightly less parsimonious to presume that pre-displacement to uncoiling approximately halfway through the first year of growth evolved twice – once in the *V. lumbricalis* (=*knorrii*) + *V. spirata* clade and once in the *V. woodringi* + *V. fargoi* clade.

Gould (1968, 1969) noted that the Walsingham Pond population of *V. spirata* resembled small *Turritella* "in all respects" but would uncoil and attach if transplanted into the presence of *Oculina* corals. It is unfortunate that the lineage appears to have been extirpated (Anderson et al. 2018) as it would have represented an interesting case for studying the hormonal or gene expression changes associated with uncoiling. Interestingly, Gould did not return to this example of paedomorphosis, which he interpreted purely adaptationally (1968;1969), when writing *Ontogeny and Phylogeny* (1977). The Walsingham Pond population undergoes post-displacement of uncoiling combined with progenesis (decreased lifespan and smaller size, and presumably earlier reproduction). The post-displacement of uncoiling was likely a loss of ontogenetic determinism while maintaining whatever host-related signaling pathway permitted them to uncoil in the presence of *Oculina*. Progenesis in the population was likely due to r-selection rather than selection for turritelliform shell, as the anchialine pond is a highly unstable environment (Geary 1988; McNamara 1988a; Thomas et al. 1991); the species is at least occasionally superabundant (the sediment at the bottom of the pond is approximately half dead *Vermicularia* shells and half organic rich mud), and mollusciverous predators are limited (Thomas et al. 1991)). The occurrence of reef masses of *V. spirata* in several localities from the Carolinas to Florida (Pearse and Williams 1951)(Anderson et al. 2018) also suggests that the paedomorphic form is not simply due to the absence of host corals (in an evolutionary sense). Plasticity in the timing or cues for uncoiling in various *Vermicularia* species may suggest that uncoiling is a form of heterocyberny, where forms induced by environmental cues in ancestral species or populations became fixed over time, expressed even in the absence of environmental cues (Bateman 1959; West-Eberhard 2003, 2005; Pigliucci et al. 2006; Gilbert and Epel 2009).

Conclusions

Few other studies have met all requirements necessary to properly test heterochronic hypotheses. Those that do typically find organisms to be heterochronic mosaics (McNamara 1988b; Jones and Gould 1999; Jaecks and Carlson 2001) with respect to different features or find peramorphic and paedomorphic processes to occur in similar frequency within a clade (McNamara 1988a; Landman and Geyssant 1993; Jaecks and Carlson 2001; Collins et al. 2016). It has been noted that many clades are biased towards paedomorphosis (Lindberg 1988; Landman and Geyssant 1993; Allmon

1994), leading to the hypothesis that paedomorphosis has a higher rate of success due to the previous success of that form earlier in the ontogeny of the ancestor (McNamara 1988a; Landman and Geyssant 1993; Allmon 1994), while peramorphic forms may extend into the unworkable (Gould 1977). Gould and Robinson (1994) noted that return to coiling (paedomorphosis) may be facilitated in *Vermicularia* as they have never fully lost the feature, and thus (unlike vermetids) are exempted from “Dollo’s Law” (that complex features are unlikely to re-evolve once lost). However, Dollo’s “Law” may not be as prevalent as assumed, or the genetic changes necessary to “re-evolve” a feature may be less dramatic than expected from the observed morphological change. The re-evolution of shell coiling and even of feeding larvae (though the latter has been considered to be particularly rare from the presumed associated loss of complex larval characters) appears to occur relatively frequently in calyptraeid gastropods, although non-feeding or direct developing larvae are observed to go through a similar sequence of larval development despite not being in the plankton (Collin and Cipriani 2003; Collin 2004; Collin et al. 2007; Collin and Miglietta 2008; Abouheif et al. 2014).

The bias towards peramorphic processes in the evolutionary history of *Vermicularia* described here is therefore striking, but it is consistent with a bias towards peramorphic forms in non-*Vermicularia* western Atlantic turritellid evolution (Allmon 1994). Allmon (1994) hypothesized selection for larger shell size or chance as possible explanations for this pattern. Future examination of sculptural characters in the Miocene-Recent *Torcula* + *Vermicularia* clade on both sides of the Atlantic would provide a valuable bridge between Allmon (1994) and this study, and could shed insight on the origins of *Vermicularia* and especially whether *V. milleti* represents an independent origin of uncoiling in turritellids (Anderson et al. 2018).

Future applications

Integration of developmental genetics with phylogenies including fossils and information from sclerochronology (with reliability tested by isotopic information or some other indicator of extrinsic time) has the potential to greatly improve our understanding of molluscan evolution (Jones 1988; Allmon 1994; Jones and Gould 1999; Goodwin et al. 2008), an important subject as molluscs are presently considered to be the most diverse phylum of marine organisms and have an extensive fossil record (Rosenberg 2014). Evo-devo studies typically focus on a few species that are well characterized and easily bred (Thewissen et al. 2012) and “the list of lab-friendly molluscs is short” (Jackson and Degnan 2016). As *Vermicularia* undergo an ontogenetic transition to an uncoiled form they provide a potential system for determining what cues may be involved in maintaining shell coiling by examining gene expression (McNamara and McKinney 2005; West-Eberhard 2005) before and after uncoiling. This information could then be compared to regularly coiled turritellids, turritellids with loose coiling in late ontogeny, and other uncoiled gastropods such as the Siliquariidae, to gain a better understanding on how uncoiling or regular high-spired coiling are controlled.

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Chapter 4: When domes are spandrels: on septation in turritellids (Cerithioidea) and other gastropods[1]

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Abstract— Although generally considered rare in gastropods, septation has long been noted in turritellids, but functional hypotheses do not survive strong scrutiny. Here we outline a methodology for testing spandrel hypotheses and apply it to the problem of turritellid septa. We follow Gould in using “spandrel” as a term for all features that are nonadaptive sequelae of adaptive features of organisms, including those that are structurally necessary, those that are developmentally correlated, and nondeterministic by-products that are correlated to features under selection.

In turritellids, septa are constructed in microstructural continuity with secondary thickening of the shell, are highly variable features infraspecifically, and are strongly associated with degree of shell thickening. We therefore conclude that rather than being themselves adaptive, turritellid septa are spandrels of shell thickening. Turritellid septa are composed of crossed lamellar aragonite, which appears to be constructed by mantle epithelium over the visceral mass. Septation was also found in 22 of 24 gastropod families examined from a broad phylogenetic distribution. Septa thus appear to be a widespread feature of caenogastropods, in strong contrast to the assertions that septa are less common in modern or high-spired shells.

INTRODUCTION

Although septa are frequently considered absent or rare in the shells of gastropods (Majewske 1974; Ray 2008; Cook et al. 2015), septation has long been noted in some groups, especially the family Turritellidae (Lyell 1838; Stimpson 1851; Andrews 1971; Allmon 2011) and some Paleozoic forms (e.g., Euomphaloidea, Murchisonioidea, and Loxonematoidea) (Yochelson 1971; Cook 1993; Gubanov et al. 1995; Wagner, 1999; Rohr and Blodgett 2016). Phylogenetic analysis by Wagner (1999) even concluded septation to be primitive for gastropods. Yet the overall occurrence of septa in caenogastropods has never been systematically analyzed, even as molecular phylogenies of gastropod higher taxa have become available (Ponder et al. 2008; Strong et al. 2011). In this study, we consider a septum to be a continuous, nonpathological wall of shell material that completely closes off the adapical portion of the shell and leaves a void space sealed off from the body cavity (Figure 4.1); this is in contrast to cephalopod septa, which are penetrated by a siphuncle (Yochelson 1971; Gubanov et al. 1995; Dauphin 2006). We demonstrate that the phylogenetic distribution of septation in gastropods is quite broad, in both Recent and fossil taxa. Our analysis suggests that septa are either primitive for Caenogastropoda (which include 60% of living gastropod species; Ponder et al. 2008) or evolved independently in many groups, with either possibility indicating that septa are not rare in gastropods.

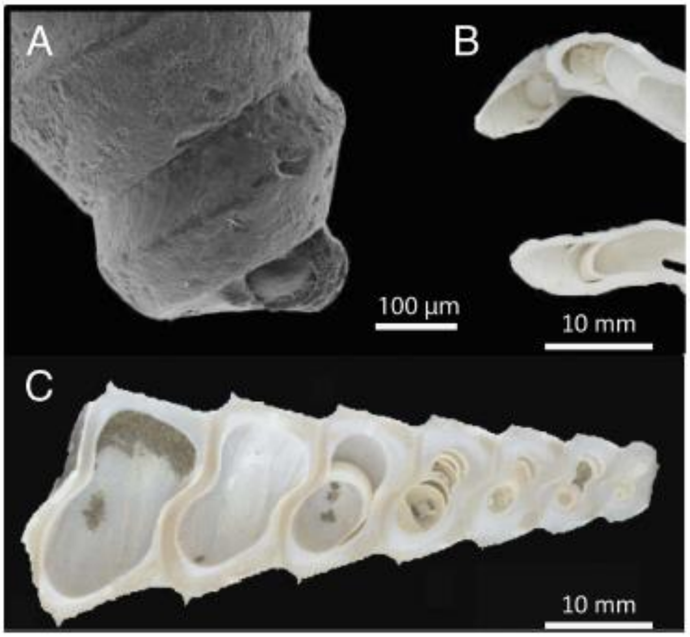


Figure 4.1 Examples of septation in turritellids. A, A dome-shaped septum visible in the apex of *Turritella altilira* (Miocene). B, Multiple septa visible in a section of *Vermicularia recta* (Plio-Pleistocene). C, Extensive septation in *T. abrupta* (Miocene).

If one's goal is to explain the origin of a particular feature of an organism, then adaptive, historical, and structural aspects all need to be considered (Seilacher 1970; Gould 2002). A variety of functional hypotheses for gastropod septa have been proposed, including: (1) response to excess calcium (Yochelson 1971; Cook et al. 2015); (2) prophylaxis against apical loss (and possible parasitic infestation; Andrews 1974; Dattilo et al. 2016); (3) protection from apex-damaging predation (Gubanov et al. 1995); (4) repair after damage (proposed and rejected in Andrews [1974]); or (5) strengthening of the shell (Yochelson 1971; Gubanov et al. 1995). Septation has also been noted to be associated with secondary shell thickening in Paleocene turritellids (Andrews 1971, 1974; Allmon 2005; Cook et al. 2015). We expand on this observation to propose that these dome-like structures are not themselves adaptive, but rather are associated with adaptive shell thickening in turritellids, and are therefore constructional artifacts—“spandrels” (sensu Gould and Lewontin 1979).

On the Definition of “Spandrels”

Use of the term “spandrel” in biology has been controversial (Houston 1997; Pigliucci and Kaplan 2000); it has, however, achieved widespread use (Gould 1997; Houston 1997, 2009; Lloyd 2013) for “sequelae of adaptive decisions” (Gould 2002: p. 1250), and we here refer to nonadaptive sequelae of adaptive features as spandrels, following Gould’s use (e.g., “Non-adaptive side consequences (‘spandrels’ in my terminology)” [2002: p. 513]). Spandrels (by-products) are epiphenomena of whatever is being selected for, and may themselves be adaptive, neutral, or maladaptive, but will persist as long as overall fitness is increased. If neutral (nonadaptive) features are effectively invisible to selection, they may persist for long periods (Gould 2002: p. 1247). We choose this terminology in agreement with Gould (1997), who considered the term “spandrel” to be “the most obvious, the most useful, and the most historically sanctioned term available” for predictable forms that arise as consequences of other features, rather than as direct adaptations. The term is used herein in the broad sense to encompass three types of spandrels (delineated herein): (1) purely geometric consequences (Gould and Lewontin 1979), sometimes considered spandrels sensu stricto (Houston 2009); (2) coupled developmental consequences (Gould and Lewontin 1979) (in which selection for one downstream target results in additional consequences that may be either selectively neutral or detrimental, so long as the primary target generates net positive fitness (e.g.,

Table 4.1. Classification of types of spandrels.

	Name	Description	Level of Determinism	Example
Type I	Geometric/ Architectural /physical Consequence	A feature that originates as a geometric consequence of the existence of another feature or set of features.	Necessary in the strictest Sense	• architectural spandrels between arches are roughly triangular, *by necessity* • The color of chemical compounds • Changes in surface are: volume ratios with size change • Raised withers of *Megaloceros giganteus* (Gould 1997)
Type II	Developmental Consequence /Correlate	A feature that originates as the result of selection on another feature with which it shares up-stream developmental regulatory elements	Necessary unless additional regulatory systems evolve to distinguish downstream targets. Predictable in a given genetic background.	• Penniform clitoris in Hyenas (*Crocuta crocuta*) (Gould 1981)
Type III	"Correlation of Growth"/ sequelae	A feature that originates as the result of selection for of another related feature in the species, but which is not a *necessary* byproduct. The feature which is the spandrel may be highly variable, but closely associated with the related feature in the species or individual.	Not necessary in the philosophical sense. A result of another feature in the organism or species, but the relationship is probabilistic rather than deterministic. A pure "byproduct" or "accident" in the sense of "things falling together".	• Cultural equivalent- cannibalism in Aztec Society (Gould and Lewontin 1979) • Female orgasm (Gould 2000b, p. 1262; Lloyd 2013) • Polydactyly in large dog breeds (Alberch 1986) • Writing (Gould 1997, 2000b)

Gould 1981); and (3) any other by-products of features under selection, determinant or indeterminate (Gould and Lewontin 1979; Gould 1997; Table 4.1).

Type 1 spandrels are sometimes called “Gould-Lewontin spandrels” or “true spandrels” (Houston 2009), but this is an incorrect attribution that results from taking the metaphor more literally than did the authors themselves. Gould and Lewontin (1979) explain that in architecture spandrels are tapering triangular spaces formed by the intersection of two rounded arches at right angles, and are necessary architectural by-products. The necessary aspects are the number (one between each arch, four when mounting a dome on four arches) and the shape (roughly triangular) (Gould 2002: p. 1250). The analogy in Gould and Lewontin (1979) is that spandrels are by-products of selection for something else and that the form of this by-product is not itself selected—not that spandrels only refer to sequelae that are “necessary” in the ontological sense (contra Houston 2009). Architectural spandrels are often exapted (Gould and Vrba 1982) for decoration. In their 1979 paper outlining the concept, Gould and Lewontin also draw an allusion to cannibalism in Aztec society—“a system developed for other reasons resulted in an increasing number of fresh bodies; *use might as well be made of them*” (emphasis added). Cannibalism, Gould and Lewontin argued, originated as a by-product (albeit a functional one), rather than a necessary and unavoidable consequence of hierarchical or militaristic society.

In a biological sense, when outlining nonadaptationist evolutionary research programs, Gould and Lewontin (1979) make explicit reference to the fact that the essential aspects of a biological spandrel are (1) there is no selection for the part directly, and (2) the “form of the part is a correlated consequence of selection directed elsewhere … Darwin ranked his ‘mysterious’ laws of the ‘correlation of growth’… Today pleiotropy, allometry, ‘material compensation’ (Rensch 1959)” (p. 591). Houston (2009) argues that by removing architectural necessity from the definition of a spandrel, it becomes redundant with the term “by-product.” Spandrels, however, are only used to refer to by-products of selection for some other feature, excluding features that originate as by-products of genetic drift, environmental limitations, and so on. Additionally, the term “spandrel” is reserved for forms that are in some sense *predictable* consequences (Gould 1997). In any case, the term is meant primarily to clarify the importance of distinguishing historical origin from present utility, as well as providing a nonbiological metaphor for nonadaptive by-products of adaptive features (Gould 1997).

It has sometimes been argued that such features are themselves adaptive, or are not strictly the only option, given a constraint (implying strict necessity is essential to the definition) (e.g., Houston 1997, 2009). Referring to the architectural example, Houston (1997, 2009) argues that the pendentives (the specific architectural term for the roughly triangular spaces between a dome and its base, as opposed to spandrels, which can refer to any roughly triangular connective region, but most typically to that between adjacent arches; Mark 1996; Gould 1997; Houston 1997, 2009) employed in San Marco are adaptive, because a design based on squinches (arches or corbelings that transition between a square planned space and a dome; Mark 1996; Houston 2009) would likely collapse. This misses the point—if no medieval architect would employ squinches due to the likelihood that the dome would collapse, this does not make pendentives adaptive in metaphor—they were chosen because they were presumed to be necessary sequelae of constructing a dome of that size. Gould and Lewontin (1979) did not argue that pendentives did nothing useful (Gould 1997). In the metaphor, the adaptationist error was presuming the spandrels were there *to house images*, even if these were not part of the original design (Gould 1997). The aspects that make them spandrels, in the Gould and Lewontin sense, are that they have properties, such as number, size, and approximate shape, that are consequences of the primary reason for building a structure (Gould 1997). If other possible constructions would cause collapse of the dome, that does not mean they are also selected independently of the decision to construct the dome. Such logic would lead one to conclude, for example, that selection for greater limb length also means specific selection for having more skin, as exposed internal organs are maladaptive, but it would be uninformative to treat the two as equally important in understanding the selection pressures present in the history of the organism. Similarly, pendentives are superior to spaces left open if they do nothing other than keep out the rain (Gould 1997). Gould considered the reading that San Marco's pendentives are adaptations "seriously false and based on a misreading of [their] clearly stated intent" (Gould 1997). The pendentives of San Marco are spandrels in the sense that the basic physical features are "secondary consequences, not primary intents" (Gould 1997).

Gould was especially explicit in other writings that "spandrel" certainly encompassed type 2 and 3 spandrels as well and treated "by-product," "non-adaptive sequelae," and "spandrels" as synonyms (Gould 1997, 2000b, 2002: pp. 43, 1250). Gould (2002: p. 87) states that "the spandrels of the human brain must greatly outnumber the immediately adaptive reasons for increase in size," and it is nonsensical to interpret his meaning to be that the music of Brahams, Bach, and Beethoven was *a physically necessary* by-propduct of large brains, in the strict geometric sense to which others have sought to circumscribe the meaning of spandrels.

It has been argued that spandrels are a hypothesis of last resort, result from lack of imagination, or that such hypotheses are simply unfalsifiable. Pampush and Daegling (2016), for example, treat multiple spandrel hypotheses for the origin of the human chin as being "resistant to tests," despite themselves providing in the same paper either strong arguments against several spandrel hypotheses (not all of which would here be classified as spandrels, but which are nonadaptive) or showing that these hypotheses have not been well demonstrated with affirmative evidence in their favor. We agree with Lloyd (2013) that nonadaptive explanations, including spandrel hypotheses, should be tested alongside adaptive hypotheses on equal footing. Spandrel hypotheses should not be considered the null hypothesis, but neither should adaptive explanations be favored "over non-adaptive accounts without good evidence for doing so, or, indeed, against the evidence" (Lloyd 2013: p. 29). Spandrel hypotheses are not the default position when adaptive explanations fail; they are positive alternative causal hypotheses that can be tested (Lloyd 2013). In the following section we outline a methodology for testing whether a feature is a spandrel.

Testing Hypotheses for the Origin of an Observed Feature

The hypothesis that a feature is a spandrel is not a null hypothesis. To demonstrate that a feature is a spandrel it must be shown that:

1. 1. The proposed spandrel is correlated to another feature.
2. 2. There is at least plausible selection for the correlated feature.

Additional supporting evidence that might favor diagnosis of a spandrel varies by the type of spandrel:

Type 1 spandrels:

As these spandrels are necessary in the strict sense, evidence needs to be gathered with respect to which feature is under selection, unless the necessary aspect is demonstrably unidirectional (e.g., dramatic enlargement of antlers require raised withers to support the head of *Megaloceros giganteus*, but enlarged withers would not necessitate drastically enlarged antlers for the organism to function; Gould 1997)

Type 2 spandrels:

1. 1. Shared regulatory genetic elements between the hypothesized spandrel and the correlated selected feature could be identified.
2. 2. Demonstrating that the spandrel is maladaptive in isolation from the correlated feature that has been selected provides strong evidence that the feature is a spandrel. The hypothesized spandrel may be selectively neutral, but if it is maladaptive, the evidence is stronger that it does not have an unknown, beneficial function. As Gould and Lewontin (1979) predicted, because adaptationists do not consider nonadaptive explanations affirmative answers and are always capable of proffering additional adaptive explanations, these hypotheses are often favored even without evidence. As Lloyd (2013) describes,

“There is no stopping rule to the question ‘what is the function of this trait?’ as opposed to the question ‘why is this trait present in an organism?’”

Type 3 spandrels:

1. There must be sufficient variation in the hypothesized spandrel to demonstrate the feature is not itself under strong selection (Van Valen 2009), for example, high phenotypic variation in female orgasm (Lloyd 2013).

2. There must be evidence of strong correlation with the proposed adaptive feature, which may take the form of:

    - a. high statistical correlation to another feature
    - b. evidence of the generation of the proposed spandrel through homologous features/processes
    - c. a demonstration of direct developmental or constructional relationship (e.g., male nipples; Gould 1987)

3. A demonstration that the feature does not affect fitness itself supports the origin of the feature as a spandrel.

4. Demonstration that the proposed spandrel is correlated with the proposed adaptive feature in taxa/lineages that are phylogenetically implied to have developed the feature independently (e.g., polydactyly in large dog breeds; Alberch, 1986) also indicates that the features may be developmentally related.

If no known adaptive or phylogenetic reason explains a feature, it is not necessarily a spandrel*. In order for a feature to be a by-product, there must be a correlation to a feature under selection.* Additionally, an adaptive explanation for the *origin* of a feature (as distinct from its *current function*, which may be adaptive or exaptive; sensu Gould and Vrba 1982) would disprove the hypothesis that the feature arose as a spandrel that was not itself selected for. The absence of evidence for adaptive origin is not, on its own, evidence that a feature is a spandrel (Lloyd 2013). Both adaptive and nonadaptive hypotheses should be considered, and if there is more positive evidence that a feature is a spandrel of another feature, then a spandrel hypothesis should be favored.

When positive evidence supports a feature's classification as a spandrel, it should not be dismissed because the relative frequency of spandrels is presumed to be rare. Such reasoning is circular and amounts to favoring adaptive explanations over nonadaptive explanations, not in the absence of evidence, but in direct contravention of evidence. One is more likely to see horses in the street in Philadelphia than zebras, but if news organizations publish video of zebras that have escaped from a circus (reported by the Associated Press, 16 November 2015) and one were to claim that these were horses painted to look like zebras, the burden of proof is not suddenly transferred to those asserting the animals to be zebras. Constructing an assessment that spandrels are rare relative to adaptations with respect to the nature of features of organisms generally would be extremely problematic, as it would involve arbitrarily atomizing organisms best understood as wholes (Gould and Lewontin 1979) and somehow knowing how many traits they possess. Further, if we include as spandrels such things as every thought that any human person could potentially produce not related to whatever the original purpose of increased encephalization was (e.g., Gould 2000b) and features that are adaptively neutral at present, such as the color of various biochemicals that are not visible externally, these side consequences would necessarily overtake the adaptive features that generated them. Such contests appear arbitrary and are not relevant to the questions with which biologists typically concern themselves, for example, what led to the presence of a particular feature?

Not every nonadaptive feature of an organism is itself automatically a spandrel (Gould 2000b). Gould refers to the triangular "constructional morphology" model for aptive structures (2002: p. 1052, following Seilacher 1970), with functional, historical, and structural vertices. He divides the structural vertex into two components: "direct action of physical laws upon plastic material," and "*architectural sequelae (spandrels)* that arise as non-adaptive consequences of other features" (emphasis added). Nonfunctional features that result from genetic drift are not spandrels (in contrast to the use in Pampush and Daegling 2016). Trade-offs are a form of constraint, but not necessarily spandrels (Aiello and Wheeler 1995; Pampush and Daegling 2016). To be diagnosed as a spandrel, a feature must originate as a direct sequel, consequence, or by-product of selection *for another feature*. Nor is suboptimality in one feature due to competing demands of selection on other features of the organism sufficient to designate a feature a spandrel. Constraint in total metabolic activity should not be considered sufficient to designate reduction of one feature a spandrel of expansion of another, if the two are not demonstrably inversely correlated and developmentally associated in some way. The argument that an organism has a limited supply of total energy is weak and does not imply that the reduced feature was the only option for offsetting the additional cost of the enlarged feature, and this reduction could itself be viewed as “adaptive” for saving energy, if that is a new selective pressure.

MATERIALS AND METHODS

To assess the phylogenetic distribution of septa in extant caenogastropods, 10 phylogenetically diverse families were examined (taxa indicated in Supplementary Table S4.1). These families were chosen to represent high- to medium-spired gastropods from a broad phylogenetic distribution, following Ponder et al. (2008). The Recent mollusk collection at the Paleontological Research Institution was surveyed, and exemplar specimens were chosen based on apical completeness. During this survey, septa were frequently observed in broken specimens; however, the possibility that these were constructed in response to damage during the life of the organism could not be excluded by examining these specimens. As apical completeness was rare (Johnson et al. 2017), most non-turritellids examined in this brief survey were single examplars. The limited nature of this survey (single species, typically single specimens) would therefore bias our examination against detecting septa if they are only occasionally present in some families. These were supplemented with information from the literature. Micro–computed tomography (CT) scans were performed with a GE CT-120, and nano-CT scans were performed with a Zeiss-Xradia Versa 520 to determine the presence/absence, morphology, and insertion of septa.

Eight Recent turritellid species (*Turritella communis* Risso, 1826; *T. duplicata* Linnaeus, 1758; *T. leucostoma* Valenciennes, 1832; *T. terebra* Linnaeus, 1758;

Turritella variegata Linnaeus, 1758; *Maoricolpus roseus* (Quoy & Gaimard, 1834); *Stiracolpus pagoda* Reeve (1849); *Zeacolpus vittatus* (Hutton, 1873) and two fossil species (*T. abrupta* Spieker, 1922=*T. robusta* Grzybowsk, 1899; *T. subannulata* Heilprin, 1887), were laterally sectioned using a wafering saw. Seven *Turritella leucostoma*, all of adult size, were sectioned to evaluate intraspecific variation in septal insertion and examine the possible association with secondary thickening of the shell. Six *Terebra dislocata* Say, 1822 (Conoidea: Terebridae) were also sectioned for comparison. Whorls were measured with a digital caliper at the midpoint of each whorl to determine whorl thickness and across the exterior of each whorl between midpoints to determine whorl width. The percent filled of a whorl was calculated as twice the thickness divided by whorl width times 100.

Turritellid septa were confirmed to be aragonitic using Raman spectroscopy, a nondestructive technique that can distinguish among aragonite, calcite, and vaterite (Frech et al. 1980; Urmos et al. 1991; Wehrmeister et al. 2010; Olcott Marshall and Marshall 2015; Supplementary Figure S4.1). Spectra were acquired with a Renishaw InVia microRaman system housed at the Cornell Center for Materials Research using the 785 nm laser, with 10 s acquisition times, and between 5 and 10 accumulations to obtain good signal-to-noise ratio.

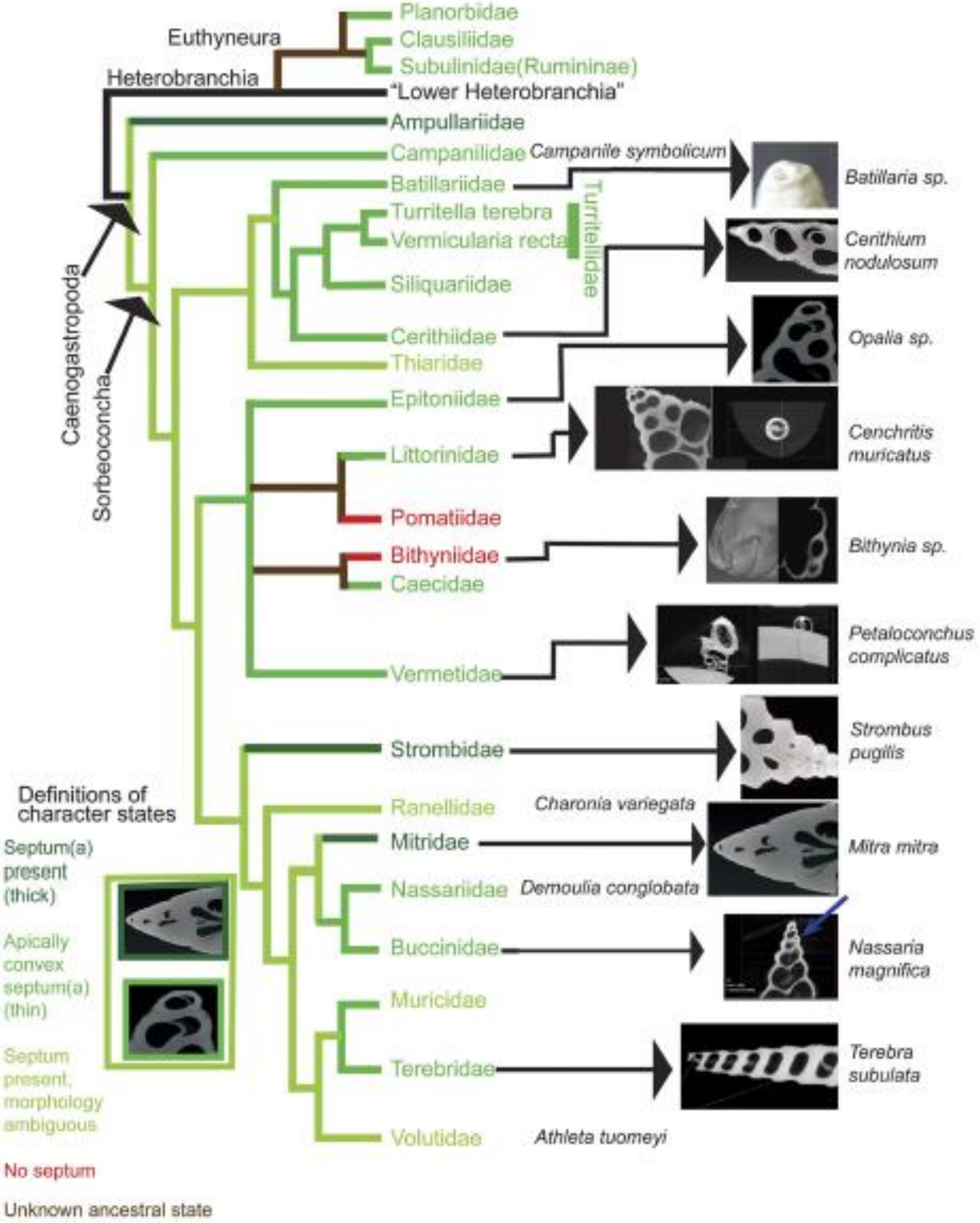
Scanning electron microscopy (SEM) was conducted using a JEOL JCM-5000 Neoscope. SEM images were obtained without any conductive coating. Where noted, specimens were etched using 10% glacial acetic acid for 20 s. All sectioned turritellids, *Cerithium eburneum* Bruguière, 1792 (Cerithioidea: Cerithiidae), and *Terebra variegata*

Gray, 1834 (Conoidea: Terebridae) were examined to assess microstructure and the morphology of the contact between septa and the inner shell wall.

RESULTS

Septa were observed in 10 of the 12 families examined, the exceptions being the Bythiniidae and Pomatiidae (Figure 4.2). Combined with information available in the literature reporting septa in Planorbidae (Brown et al. 1984), Subulinidae (Rumininae) (Hochpöchler and Kothbauer 1975), Clausiliidae (Pall-Gergely and Nemeth 2008), Campanilidae (Houbrick 1981), Thiaridae (Fretter and Graham 1962), Caecidae (Fretter and Graham 1962), Ranellidae (Bandel 1979), Nassariidae (Fortey 2009), Volutidae (Ford 2006), and Muricidae (Bandel 1979), septa appear to be a widespread feature of Caenogastropoda, with thin, apically convex septa the most common form. Septa in turritellid gastropods are very thin, only 0.14–0.25 mm thick, with thicker septa (0.50–0.90 mm) composed of multiple layers, often with gaps between these layers (Figure 4.3, Supplementary Figure S4.2). In some groups (Mitridae, Volutidae, Strombidae), septa are thick and may form through different processes (e.g., *Strombus* fill their apices, and septa may be generated through temporary cessation of deposition; Figure 4.2). The presence of septa in a wide variety of taxa, including heterobranchs, basal caenogastropods, littorinomorphs, cerithiods, and neogastropods, suggests that they are either plesiomorphic for caenogastropods or extremely commonly evolved in unrelated taxa.

Figure 4.2. Phylogenetic distribution of septa in caenogastropods. Supertree phylogeny of caeonogastropods based on the strict-consensus tree obtained from Bayesian analysis of the combined molecular and morphological data set performed by Ponder et al. (2008), with modification to cerithioidean relationships based on Strong et al. (2011), and the positions of Pomatiidae, Caecidae, and Buccinidae inferred based on the superfamilial relationships in Bouchet et al. (2005). Data for Siliquariidae (Bieler 2004), Planorbidae (Brown et al. 1984), Subulinidae (Rumininae) (Hochpöchler and Kothbauer 1975), Clausiliidae (Pall-Gergely and Nemeth 2008), Campanilidae (Houbrick 1981), Thiaridae (Fretter and Graham 1962), Caecidae (Fretter and Graham 1962), Ranellidae (Bandel 1979), Nassariidae (Fortey 2009), Volutidae (Ford 2006), and Muricidae (Bandel 1979) were obtained from the literature. Septa were detected in all other taxa using CT scans, SEM, or visual observation. Ancestral states inferred through parsimony. Green colors indicate that septa are present. Light green indicates taxa in which the septum is thin and apically convex. Dark green indicates taxa in which septa are thick. Yellow-green indicates taxa that possess septa of ambiguous morphology. Red indicates taxa that were examined and found not to possess septa. Brown indicates unknown ancestral states. Consult Supplementary Figure S4.6 for enlarged images.


Euthyneura
Heterobranchia
Planorbidae
Clausiliidae
Subulinidae(Rumininae)
"Lower Heterobranchia"
Ampullariidae
Campanilidae
Campanile symbolicum
Batillariidae
Batillaria sp.
Turritella terebra
Vermicularia recta
Turritellidae
Siliquariidae
Cerithium nodulosum
Caenogastropoda
Sorbeoconcha
Cerithiidae
Thiaridae
Opalia sp.
Epitoniidae
Littorinidae
Cenchritis muricatus
Pomatiidae
Bithyniidae
Bithynia sp.
Caecidae
Vermetidae
Petaloconchus complicatus
Strombidae
Strombus pugilis
Definitions of character states
Septum(a) present (thick)
Apically convex septum(a) (thin)
Septum present, morphology ambiguous
No septum
Unknown ancestral state
Ranellidae
Charonia variegata
Mitridae
Mitra mitra
Nassariidae
Demoulia conglobata
Buccinidae
Nassaria magnifica
Muricidae
Terebridae
Terebra subulata
Volutidae
Athleta tuomeyi

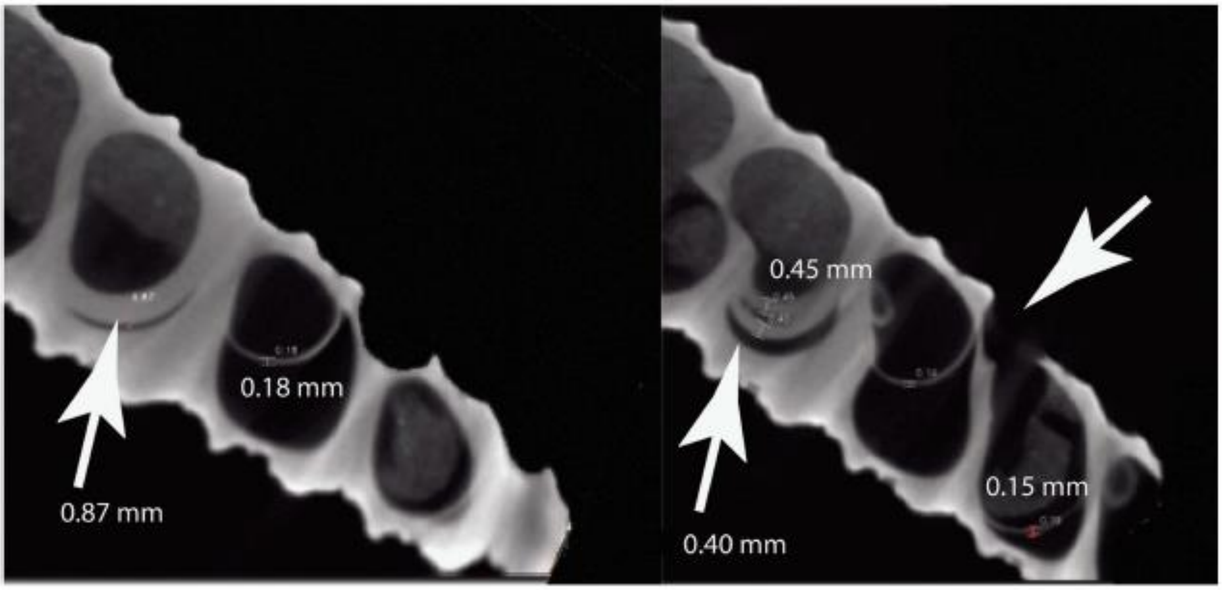


Figure 4.3. Nano-CT scan of *Turritella altilira* from the Miocene, Gatun Formation (Panama). The septum in the left panel appears thick (0.87 mm), but is in fact composed of multiple layers of septa, with a gap evident in a deeper transect (right panel), location indicated with arrows. An additional arrow in the second panel shows the presence of a predatory drill hole located adapically of a septum, the sole instance of possible predation failure due to septa observed in 1263 shell fragments examined in Anderson et al. (2017).

Turritellid septa universally have aragonitic crossed-lamellar (Lowenstam and Weiner 1989) microstructure (Figure 4.4), with some showing limited deposition of simple lamellar fibrous structure, as in the transition observed in the septa of the ranellid *Charonia variegata* Lamarck, 1816 (Bandel 1990). We also observed this microstructure in the inner shell layer of turritellids and in the material deposited by *Turritella abrupta* and *T. duplicata*, which sometimes fill their apices completely (Figure 4.1, Supplementary Figure S4.3). Crossed-lamellar microstructure is the most common microstructure in mollusks (Salinas and Kisailus 2013; Voltzow 1994), but has a high degree of order (Salinas and Kisailus 2013), requiring a complex interaction with organic macromolecules (Weiner et al. 1984; de Paula and Silveira 2009; Nouet et al. 2012; Hickman 2013). In both turritellids and other taxa, septa form in clear continuity with the inner shell layer, with lamellae continuous in orientation where they intersect the inner shell layer (Figure 4.4B), and septa maintain crossed-lamellar microstructure even at the apex of the dome (Figure 4.4). The microstructure of septa from two non-turritellid taxa—*Cerithium eburneum* (Cerithioidea: Cerithiidae) and *Terebra variegata,* (Conoidea: Terebridae)—were also examined and found to be crossed lamellar (Supplementary Figures. S4.3, S4.4), consistent with reports of crossed-lamellar microstructures in the septa of *Charonia variegata* (Bandel 1979, 1990). Septa in *Cerithium eburneum* also appear to form in continuity with an inner shell layer, although for *Terebra variegata* this relationship is less clear, with a thin innermost shell layer in continuity with septa (Supplementary Figure S4.4C).

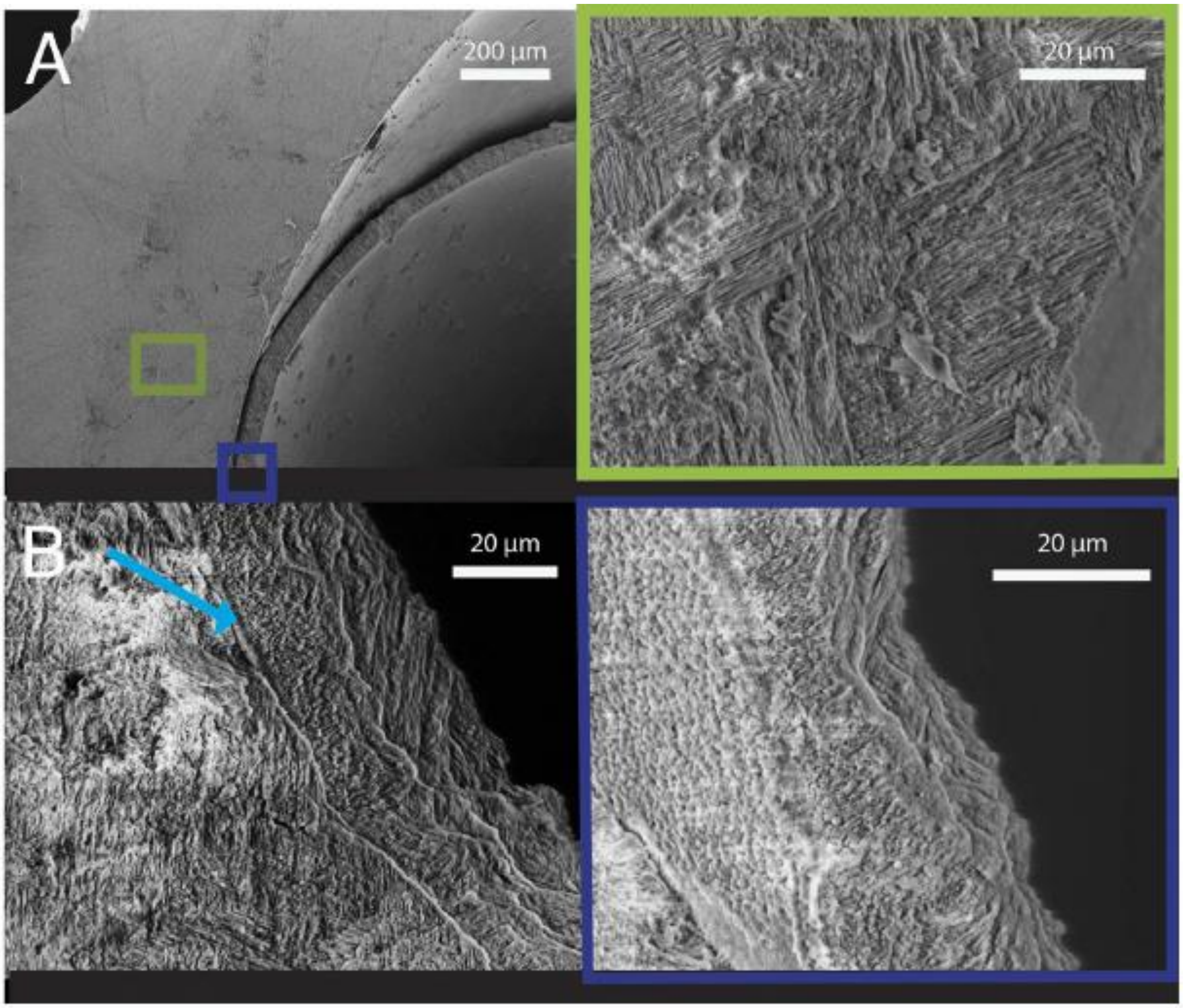


Figure 4.4 The microstructural relationship between septa and secondary shell deposition in *Turritella terebra*. A, Overview showing the relationship between outer and inner shell layers and a septum. At right is a magnified view of the region indicated with the upper (green) rectangle, showing crossed lamellar microstructure. B, Detail of the region where the septum first detaches from the inner shell layer (left). This shows that septa form in continuity with the microstructure of the inner shell layer (boundary indicated with an arrow) before becoming distinct (right, region indicated by the lower, blue box in A), but maintain crossed-lamellar microstructure.

Septa are not inserted at regular intervals in *Turritella leucostoma*, and there is no obvious pattern to the position where they are inserted (Supplementary Figure S4.5). Further, the number of septa in each similarly sized shell is highly variable (mean=7; SD 2.85). At 39.9% of the mean, this standard deviation exceeds the 10% coefficient of variation threshold proposed by Van Valen (2009) for detecting traits not themselves maintained by selection. Septa are rare in *Terebra dislocata*, with only one individual sectioned found to possess two septa in total, in the second and third teleoconch whorls.

A clear relationship exists in turritellids between septation and the extent of secondary thickening of the shell (Tables 4.2, 4.3). Across all turritellid species examined, septa are more likely to occur in whorls where a greater portion of the whorl has been secondarily filled (Table 4.2; mean % filled 39.51 and 21.62 for septate and nonseptate whorls, respectively; *t*-test *p*<0.0001). In whorls of multiple individuals of *T. leucostoma*, septa were found to also be associated with thickening (Table 4.3). Septa are associated with more substantially thickened whorls even when only potentially septate whorls are considered (mean % filled 46.4 and 38.2 for septate and nonseptate, respectively; *t*-test p=0.0018; see Table 4.3 for additional treatments). *Terebra dislocata* had a noticeably lower mean % filled compared with most turritellid species examined (Supplementary Table S4.2), but the difference between septate and nonseptate whorls in the first three teleoconch whorls was statistically significant (mean % filled 32.2 and 23.4%, respectively; *t*-test, *p*=0.01).

Table 4.2 Comparison of percentage of whorl filled between whorls with and without septa for non–*Turritella leucostoma* turritellid species. Percent filled measurements are included multiple times when multiple septa were present in the same whorl. Solid filled whorls are excluded. Bold indicates *p*-values significant at a 0.05 threshold.

Species	# of septa present	Mean % filled Septum present	Mean % filled Septum absent	t-test *p* value
T. communis	4	58	22	**0.0010**
T. subannulata	3	55.33	21	**0.0012**
T. terebra (large)	11	23	16	**0.0399**
T. terebra (small)	11	35	18.8	**0.0099**
T. variegata	3	49	22.38	**0.0144**
Zeacolpus vitatus	4	59	22.75	**0.0088**
Stiracolpus pagoda	3	38.67	23.29	**0.0464**

Table 4.3 Comparison of % whorl filled between whorls with and without septa for seven *Turritella leucostoma* under varying conditions. “By whorl” indicates that multiple septa within a single whorl were treated as a single septate whorl and compared with nonseptate whorls, whereas “By septum” indicates that multiple septa were treated individually. Bold indicates *p*-values significant at a 0.01 threshold.

Aggregate of all non-*T. leucostoma* species	39	39.51	21.62	**< 0.0001**
Test condition	N septate condition/N non-septate	Mean % filled Septum present	Mean % filled Septum absent	**t-test p value**
By whorl	37/33	44.8	33.0	**0.0010**
By whorl; only in region where septa are found	37/12	44.8	38.2	**0.0080**
By Septum	50/33	46.4	33.0	**0.0010**
By Septum; only in region where septa are found	50/12	46.4	38.2	**0.0022**

DISCUSSION

Most functional hypotheses for septation in turritellids (see “Introduction”) do not survive strong scrutiny. Only prophylactic hypotheses, particularly the possibility that septation reduces risk of microbial infection via seawater, are consistent with the available data.

1. If septa function for carbonate sequestration, then this role is already served by thickening the shell and should be uncommon in turritellids from low-carbonate environments, such as *Turritella communis*. Further, if this is a sink to avoid hypercalcemia (Yochelson 1971), it is not intuitive why crossed-lamellar aragonite would be employed across multiple clades when less energetically expensive microstructures (Dillaman 1981; Palmer 1983; Weiner et al. 1984; Lowenstam and Weiner 1989; Avery and Etter 2006; de Paula and Silveira 2009; Cook et al. 2015) would readily serve this function.

2. The hypothesis that septa provide protection against loss of the apex and possible parasitism of the gonads/digestive glands does not explain continued septal insertion in taxa that fully plug the most apical whorls with solid shell material, such as *T. abrupta* (Figure 4.1C) and *T. duplicata* (Supplementary Figure S4.2E). Further, while castration due to parasitism is a significant evolutionary pressure for turritellids, such parasites enter through the digestive tract, rather than penetrating the epidermis of the animal (Rothschild 1935; Perez 1936; Wright 1956, 1971; Negus 1968; Bieler and Hadfield 1990; Poulin and Mouritsen 2003; Allmon 2011).

3. The hypothesis that adapical septa may be adaptive in turritellids or other gastropods to prevent seawater (and therefore microbial) access to the thinner epithelial tissue covering the visceral hump remains plausible. Yet in the hypothetical scenario in which a single septum or a small number were inserted near the apex as prophylaxis against possible loss of the protoconch/apex, the majority of septa within a typical turritellid shell would remain spandrels, as they do not serve this function (in this case, spandrels of the adaptive construction of single or limited septa). Any trauma that could sever the top 40% of a turritellid shell would not be thwarted by a 0.15-mm-thick dome. This would presumably include apex-snipping predators (hypothesis 3), which could conceivably be deterred by being forced to break larger whorls. Gastropods can also repair the shell rapidly after being damaged, patching breaches quickly with thin membranes before filling in additional shell material (Muzil et al. 1966; Marshall and Day 2001; Fleury et al. 2008; Fernández et al. 2016). It is possible that the gregarious nature of turritellids (Allmon 2011) could lead to additional selective pressure from diseases, but constructing multiple septa far from the apex appears wasteful. The idea that the epithelium of the visceral hump produces scents more enticing to predators than the rest of the animal, which is normally exposed to seawater (including excretory apparatus), does not seem plausible. Neither increased rates of infection or increased attractiveness to predators for individuals with damaged apices have been demonstrated experimentally. If these hypotheses were shown to be correct, then the insertion of septa in early

whorls would potentially be an adaptive (or exapted, depending on evolutionary history) feature.

4. Further, in examining several hundred shell fragments (1263 fragments, 74 drill holes [Anderson et al. 2017]; 3475 fragments, 128 drill holes [Johnson et al. 2017]) only a single instance of drilling predation was found to have potentially failed due to the presence of a septum (Figure 4.3). The observation of repeated septal insertion in shells with no apparent breakage or breaches of the external shell refutes the hypothesis that they are responses to damage or imminent threat (hypothesis 4).

5. The extreme thinness of gastropod septa also suggests that they do not function themselves to strengthen the shell (in agreement with Yochelson [1971] and Gubanov et al. [1995]).

For turritellids, the failure of these adaptive hypotheses, combined with high intraspecific variability (Van Valen 2009) and a strong association with an adaptive feature (secondary shell thickening—an association demonstrated by their common physical construction [Figure 4.4B] and the statistically significant association of septa with thickening both within individuals of a single species [Table 4.3] and across species [Table 4.2]), suggests that septa are spandrels (type 3). While the possibility that septal insertion is a response to an unknown, highly variable, environmental perturbation cannot be positively excluded, secondary shell thickening, an adaptive feature (Tull and Bohning-Gaese 1993), provides a sufficient explanation for the construction and evolutionary maintenance of septa in this group. The microbial prophylactic hypothesis remains plausible, but there is presently no affirmative evidence in its favor (e.g., demonstrating that the mantle epithelium covering the visceral hump is more vulnerable to infection than the rest of the animal), and as the spandrel hypothesis does have support, there is no reason to automatically defer to the adaptive hypothesis in this case.

In other gastropod groups, such as Volutidae and Strombidae, it is possible that the creation of septa is the result of a similar process to that in turritellids, except rather than thickening the entire shell, these organisms may be attempting to fill the spire (which also occurs in some turritellids; Merriam 1941; Andrews 1974). If this is the case, then a temporary cessation of deposition could similarly result in the formation of a septum, deliberately or accidentally.

We are not here arguing that septation is necessarily a spandrel in all gastropods; some may deliberately construct septa. These include Paleozoic forms such as *Fletcherviewia* Cook, 1993, which do not appear to secondarily thicken their shells (Cook et al. 2015), and especially some decollate snails that appear to deliberately weaken the shell before inserting a septum (Draper 1985), with some taxa, such as *Albinaria* Vest, 1867 and *Pontophaedusa* Lindholm, 1924, constructing a single septum (Pall-Gergely and Nemeth 2008), and others, such as *Rumina decollata* Linnaeus, 1758 (Subulinidae), repeating the process multiple times (Hochpöchler and Kothbauer 1975; Gittenberger and Povel 1995; Bandel 1996; Pall-Gergely and Nemeth 2008).

Septa, like the majority of calcium carbonate structures in gastropods, have been presumed to be constructed by mantle tissue in direct contact with the location where new shell material is being laid down (Andrews 1971; Kohn et al. 1979; Bandel 1990, 1991; de Paula and Silveira 2009; Nouet et al. 2012). Fine study of the microstructure of *Charonia variegata* indicates that septa are initially spherulitic prismatic and grade into crossed-lamellar structure, “presumably with increased mantle control” (Bandel 1979, 1990; Hickman 2013). Reported examples of remote biomineralization (Chinzei and Seilacher 1993; Checa 2000; Hickman 2013), in which mantle tissue is not in direct contact with secreted shell material, are not well ordered (Bandel 1990, 1991; Hickman 2013; see also Dillaman 1981; Kemperman and Gittenberger 1988; Checa 2000), especially when microbially mediated deposition is hypothesized (Vermeij 2014). The posterior edge of the visually distinct mantle cavity of *Turritella bacillum*, however, is 4.5–5 whorls from the apical termination of body tissue (the gonads, digestive glands, etc., all located well above the columellar muscle; Figure 4.5), and 2.5 whorls away in *Turritella communis* (Fretter and Graham 1962). This situation is not unique to turritellids; in the phylogenetically distant Campanilidae, which also insert multiple septa, the adapical edge of the mantle is located 5–6 whorls from the end of the visceral mass (Houbrick 1981). Septa therefore must be constructed by mantle epithelium tissue coating the visceral mass of the organism, which is visually and histologically distinctive from the tissue of the mantle cavity (Fretter and Graham 1962). Shell repair studies have typically examined areas of the shell that more typically shell-secreting portions of the mantle can readily access (e.g., Fleury et al. 2008; Fernández et al. 2016), although interior remodeling has been described in several groups (e.g., Kohn et al. 1979).

Comparing the shell repair capabilities of the mantle epithelium of the visceral mass in high-spired marine snails with more typical apertural repair could be a fruitful area of research for understanding the physiology of mantle tissue and gastropod biomineralization.

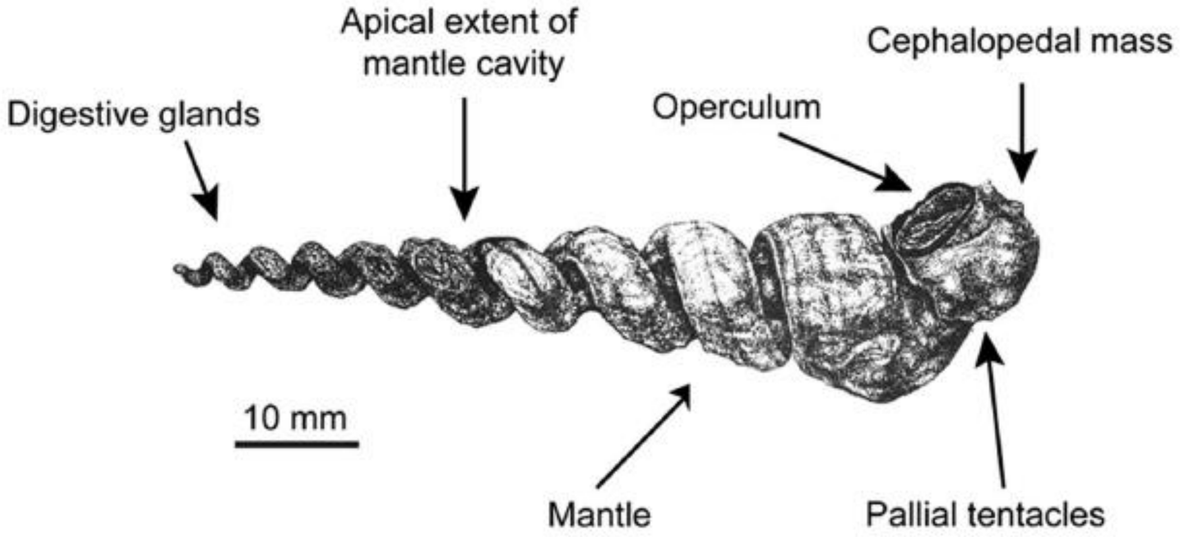


Figure 4.5. Anatomy of formalin-preserved *Turritella bacillum* animal removed from shell. Note that typical mantle tissue does not appear to extend over the last several volutions of the body (containing digestive glands and gonads).

CONCLUSIONS

Septa are widespread in caenogastropods and are also present in some shelled heterobranchs (e.g., Architectonicidae, *Heliacus implexus* Mighels, 1845 [Bieler 1993], Clausiliidae [Pall-Gergely and Nemeth 2008], Donaldinidae [Bandel et al. 2002]). Septation should be considered when examining fossil steinkerns, as the occlusion of the apex by a septum (providing it is robust enough to not be broken during the process of infilling the shell) both prevents direct measurement of the animal and provides ontogenetic information (Dattilo et al. 2016). The pervasive occurrence of septation in gastropod families also raises the question of possible homology of these structures. As gastropod septa are extremely simple in definition, we urge caution against considering all of them to be homologous, and we do not conclude that they are necessarily primitive for caenogastropods. In the case in which septa are selectively neutral epiphenomena of secondary thickening in many taxa, then they are not discrete characters (the appropriate character would be degree of shell thickening). Alternatively, if septal formation is adaptive, and the simplest means to generate septa is a generalized increase in secondary shell deposition, then the extent of shell thickening may be a spandrel of septation. Either way, separating these developmentally linked (nonindependent) characters in phylogenetic reconstructions would likely cause particular difficulties for character-poor families such as turritellids, potentially overestimating the phylogenetic relationship between species that converged on robust shells.

It also is likely inappropriate to propose simple homology of septation between septa-bearing taxa that clearly have developmental programming related to septal formation (e.g., decollate snails; Hochpöchler and Kothbauer 1975; Pall-Gergely and Nemeth 2008) and those that do not (e.g., Turritellidae). Additionally, if homologues are defined as having some underlying shared developmental programming (Wagner 2007), and no such genetic programming exists, it may be inappropriate to propose homology, even among organisms of the same species (e.g., the septum of the third whorl), if septal formation is a stochastic, rather than developmental event. Septa are, however, common features of moderate- to high-spired shells in a way that has not been heretofore appreciated.

An alternative perspective on coding septation would be to code the propensity to form septa (or to form septa sufficiently robust to be recognizable in the fossil record) separately from control on septal formation (e.g., Caecidae) and the type of control (P. Wagner personal communication). If coded in this manner, and septation is considered primitive, then loss of septation may occur either through the ability to prevent unnecessary secretion of shell material by the mantle epithelium when thickening the shell (gain of modularity) or decrease in extent of shell thickening relative to whorl expansion (spandrel of shell thickening). The absence/presence of septa would be coded as one character, agnostic to the existence of a control mechanism; the existence of a control mechanism would be a second character; and the type of control mechanism could be considered a third character.

An apparent trend toward septation in caenogastropods may be the result of either retention of the pleisiomorphic state or preferential gain rather than loss (McShea 1994) of either septation or relative shell thickening. The latter seems plausible, given increased predation pressures since the Mesozoic marine revolution (Vermeij 1977, 1987, 2013). Future work for understanding the evolution of septation in families other than Turritellidae would involve testing the correlation of septation with shell thickening among species and individuals in the respective families, determining the extent of developmental control on septal formation if it exists, and interpreting gain/loss of septation or extent of septation in a robust phylogenetic context, where ancestor–

descendant pairs or subclade tests could be performed (McShea 1994; Pagel 1994). At present, turritellid systematics are not well resolved, with the genus "Turritella" often considered a "wastebasket taxon" (Plotnick and Wagner 2006; Hendricks et al. 2014) and relationships within the family poorly understood (Beu 2010). The integration of molecular information with shell characters would be a first step toward interpreting evolutionary transitions and trends within this family.

Turritellid septa are irregularly inserted (a feature they share with septa in many other gastropod taxa, including high-spired, septate murchisoniids (Cook et al. 2015; Rohr and Blodgett 2016) and open-coiled Paleozoic gastropods, such as *Nevadaspira* (Yochelson 1971), and likely have no functional significance of their own. These domes thus appear to be spandrels of shell thickening (in agreement with the proposal that septa give "no particular advantage" to fossil Loxonematoidea (Yochelson 1971). Shell-thickening or apex-filling material may lead to septa as constructional by-products in other taxa, such as Littorinidae or *Cerithium*, with accidental septal formation less likely to occur in taxa with a faster whorl expansion rate (Raup 1966) or less extensive secondary shell thickening. Similar mechanisms may have contributed to septal formation in other taxa with similar morphology, such as hyoliths (Lophophorata) (Dzik 1978; Moysiuk et al. 2017; Parkhaev 2017). Predisposition to septal formation may have been exapted (Gould and Vrba 1982) in the uncoiled (or loosely coiled) Vermiculariinae, Siliquariidae, and Vermetidae, facilitating their rapid shell growth and uncoiled morphology and allowing the animal to remain close to the aperture (Bieler 2004), even when vertically oriented.

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APPENDIX 1: Supplemental information for chapter 1.

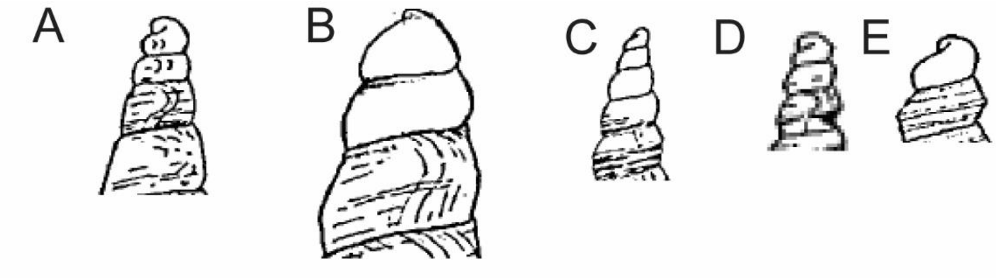


Figure S1.1. Examples of variation in turritellid protoconch morphologies (modified from Marwick, 1957a). A. *Colpospira runcinata* B. *Gazameda gunnii* C. *Kimberia kimberi* D. *Torcula exoleta* E. *Stiracolpus vittatus*

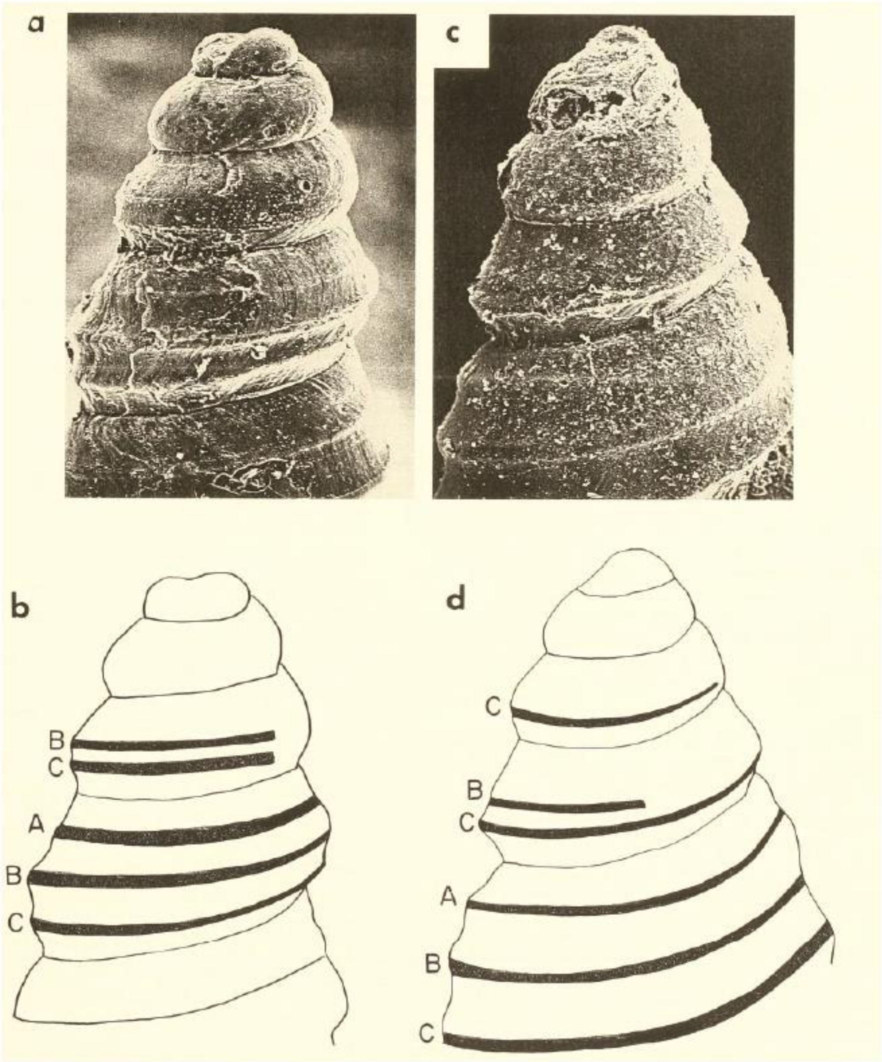


Figure S1.2. Examples of variation in the order of appearance of turritellid spiral sculpture (modified from Allmon, 1996). a. Scanning electron micrograph of *Turritella mortoni* b. Sketch indicating the onset of primary spiral cords in a. c. Scanning electron micrograph of *Turritella carinata* d. Sketch indicating the onset of spiral cords in c.

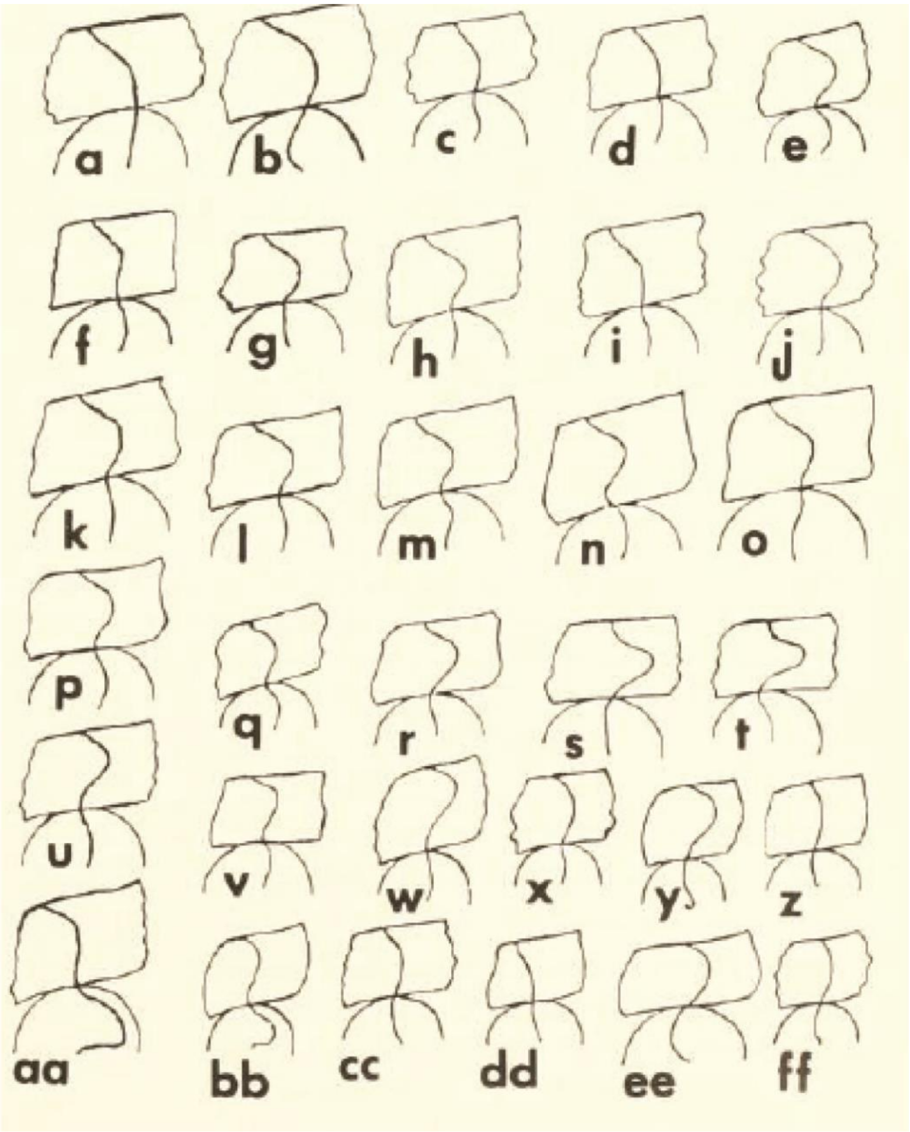


Figure S1.3. Examples of variation in turritellid lateral (top) and basal (bottom) growth line traces (modified from Allmon, 1996). All are based on type species except d, u, and aa. a. *Turritella* b. *Zaria* c. *Archimediella* d. *Torculoidella bicarinata* e. *Kurosioia* f. *Leptocolpus* g. *Ctenocolpus* h. *Gazameda* i. *Torculoidella* j. *Stiracolpus* k. *Peyrotia* l. *Maoricolpus* m. *Zeacolpus* n. *Haustator* o. *Tropicolpus* p. *Torcula* q. *Bactrospira* r. *Platycolpus* s. *Colpospira* t. *Spirocolpus* u. *Neohaustator* v. *Turritella hybrida* w. *Colposigma* x. *Colpospirella* y. *Pareora* z. *Tachyrhynchus* aa. *Protoma* bb. *Protoma* (*Protomella*) *knysnaensis* cc. *Mesalia* dd. *Neodiastoma* ee. *Sigmesalia* ff. *Glyptozaria*

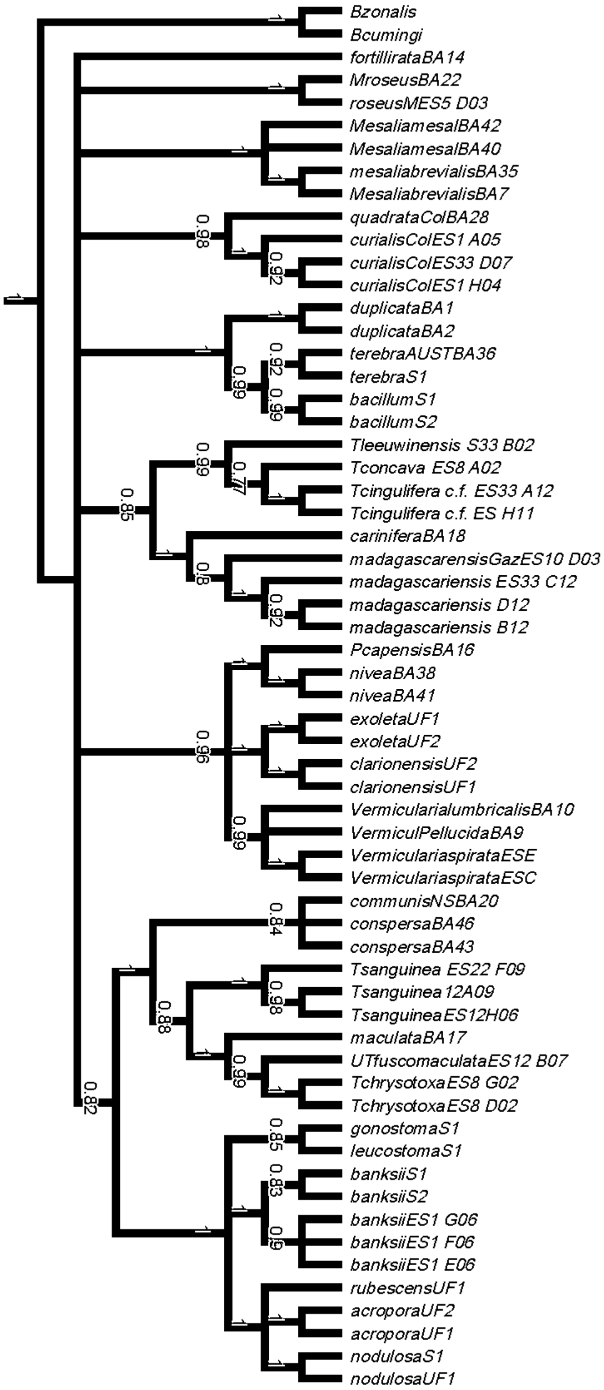


Figure S1.4. 70% bootstrap consensus of 1000 repetitions for Maximum Likelihood reconstruction constructed using RAxML, based on contatenated dataset of 12S, 16S and H3 using Batillariidae as a monophyletic outgroup.

APPENDIX 2: Supplemental Information for chapter 2

Notes on morphological characters and Morphological character state determinations

Description of shell characters

Protoconch Characters:

Protoconch data is limited, especially for fossil taxa, as protoconchs are typically lost prior to collection, even for live collected organisms (Johnson et al., 2017). Where present, protoconchs were classified according to maximal diameter (including for partial protoconchs) and whorl number.

Protoconch diameter 0= <250 μm; 1 =250 - 350 μm; 2 = >350 μm.

Number of whorls was divided into those possessing 1.25 volutions or fewer (0) and those with greater than 1.26 volutions (1). No *Vermicularia* species is presently known to have a multispiral protoconch or a protoconch of non-plesiomorphic gross morphology.

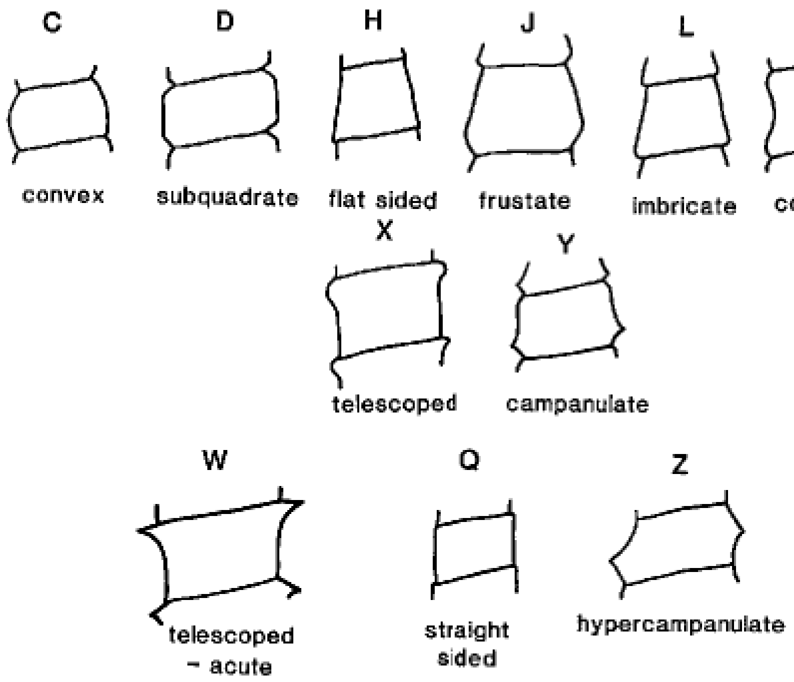
General Teleoconch characters:

Apical angle: 0 = <30 degrees; 1 = 30 degrees

Pleural Angle: 0 =10-15 degrees, 1 = 15-20 degrees, 2 = >20 degrees

Whorl profile: We used the same coding as Sang et al. (in review), following Allmon et al. 1996 definitions. 0 = convex, 1 = subquadrate, 2 = flat sided, 3 = frustate, 4 = imbricate, 5 = concave, 6 = keeled, 7 = telescoped, 8 =

campanulate, 9 = hypercampanulate 10 = straight sided, 11 = telescoped acute.



Size: Overall size was defined as the maximum length of the shell for turritellids, and the length of the turritelliform portion plus the sum of whorl widths for each complete volution in the *Vermicularia* (effectively compressing them to their size if they had been coiled). 0 = < 5 cm, 1 = 5-13 cm, 2 = 13-20 cm, 3 = > 20 cm

Suture depth: 0 = shallow, 1 = medium, 2 = deep

The presence or absence of an umbilicus forming on the turritelliform portion of the shell before uncoiling was noted.

Coloration:

Coloration of modern species was characterized as clear/white/very light or tan/dark. While several species varied in shell coloration from tan to reddish to very dark brown among individuals, the characteristic of an adult shell that is either very light (translucent or white) as opposed to pigmented was generally stable in all species. Coloration was recorded both for the apical/coiled portion of the shell and the later whorls, as early whorl color was identified separately from later coloration as this pattern is diagnostic of some species. Pattern of coloration was recorded as solid, striped, or spotted. All fossil species were coded as unknown character state for all coloration characters.

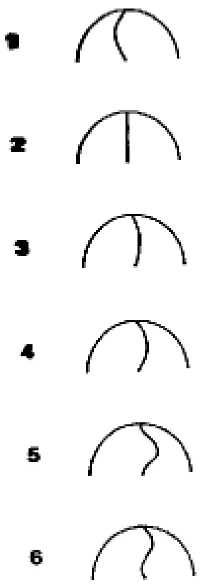
For both early and late ontogeny; Color: 0 = unpigmented, 1 = pigmented

Pattern of coloration: 0=solid; 1= vertical stripes 2= spotted or otherwise complex

Growth line Characters:

Raised or smooth: 0= smooth, 1 = raised

Basal Sinus: Defined according to Allmon (1996). 0 = Allmon type 1, 1 = 2, 2 =3, 3 = 4, 4 = 5, 5 = 6



Allmon basal sinus types

Lateral Sinus: depth 0 = shallow, 1 = medium, 2 = deep

Lateral Angle: 0 = prosocline, 1 = uninclined (straight), 2 = opisthocline

Lateral Type (Inflection points): 0 = single on bottom, 1 = double, 2 = single on top, 3 = none

Lateral Sinus Apex location: 0 = upper third, 1 = middle, 2 = lower third

Aperture shape: Gould and Robinson, (1994; also Gould, 1969) noted that free growing gastropod tubes are typically circular, but turritellid aperture shape ranges from quadrate to fully circular or teardrop shaped and *Vermicularia* species do exhibit variation in aperture shape. Aperture shape was classified as an ordered character ranging from square (0) to subquadrate (1) to circular (2) to teardrop (3). Where it could be observed, the angle between the aperture and the anterior of the previous whorl was also coded as smooth (0), prominent, near 90° or obtuse (3). Some species did not have exemplars in the pre-uncoiling stage for which this feature could be characterized.

Sculpture: Sculpture was characterized separately for early teleoconch whorls and the uncoiled (or late ontogeny for coiled species) portion of the shell. The number of major (primary) spiral chords and minor (secondary) spiral chords was determined for both early whorls and the equivalent side of the uncoiled portion in later ontogeny. Spiral ribs were divided into two types: *primaries* and *secondaries* (see Allmon, 1996). In order to be designated as a primary spiral rib (A, B, C, D), the rib must appear within 3-4 whorls of all other primaries. These primary ribs must also be the most prominent ribs and begin within several whorls of the protoconch-teleoconch boundary. Secondary spiral ribs (r', r, s, t, u) tend to appear later in ontogeny than most primary ribs. They must begin as relatively weaker than the primaries. Secondary ribs, however, are allowed to increase in relative strength compared to all other ribs throughout ontogeny. Spiral ribs are identified by relative position on the whorl. We used scanning electron micrographs whenever possible to examine the juvenile sculpture, as the position of each rib is often not constant throughout ontogeny. In alignment with Marwick's work, we first identify rib B, which appears mid-whorl. Ribs A, C, and D are identified based on their relative position to rib B. In the event that there is no primary rib near mid-whorl, we treat rib B as absent, and the space at the mid-whorl as where B should have been. We then continue identifying the other ribs. Secondaries are identified by relative position to the primaries.

The number of primary spiral ribs early and late in ontogeny was coded as 0-4, regardless of rib identity.

The number of secondary spiral ribs was coded early and late in ontogeny as 0-4, with state 4 representing 4 or more lateral ribs.

Ribs are then characterized as smooth (0) or beaded (1).

In uncoiled forms, the absence (0) or presence (1) of lineations on the exposed, formerly adapical, surface of the shell was also noted, with coiled forms coded as unknown.

Characters related to Uncoiling

The uncoiled portion of the shell was characterized according to typical range of whorl number at onset, typical width of the final coiled whorl, and whether the uncoiled portion had a wrinkled or smooth appearance. Exact whorl number/size at uncoiling appears to be partially ecophenotypic (Gould, 1968) and therefore ranges were used rather than specifying particular whorl numbers, however species do not typically exceed the ranges to which they have been classified here.

Uncoiling was characterized as atypical (0) or typical (1) of ontogeny.

Typical uncoiling diameter was coded as an unknown character in coiled species and an ordered character in uncoiled forms. It was measured at the whorl prior to the first separation as follows

≤ 0.5 cm (0), 0.5-0.75 cm (1), 0.75 – 1 cm (2), and > 1 cm (3)

The number of whorls at uncoiling is also a variable trait infraspecifically, therefore average numbers were used and divisions reflect apparent consistent groups. This was considered an ordered character from never uncoiling (0), uncoiling at >10 whorls (1), uncoiling between 7 and 9 whorls (2) or at 6 or fewer whorls (3). This last category was kept intentionally broad as early uncoiling species were also observed to be more highly variable.

The maximum observed length of the uncoiled portion was characterized as less than 3 cm (0), 3-6 cm (1), 6-9 cm (2), or greater than 9 cm (3).

The uncoiled portion was characterized as smooth (0) or wrinkled (1).

Hermatypic behavior

The frequent formation of bioherms with conspecifics was noted as characteristic of the species (state 1) or not (0), where any species which is known to form such structures frequently was coded as hermatypic (1), even if it is often found isolated or associated with other reef forming taxa as well.

Character matrix

species	protoconch diameter*	protoconch number of whorls	basal sinus shape*	lateral sinus depth*	lateral angle*	lateral type(infl points)	lateral sinus apex location*	apical angle	pleural angle*	whorl profile	Size class*	aperture shape*	Suture depth*	Raised growth lines	Uncoiling typical of ontogeny	uncoiling diameter*	uncoiling average number of whorls*	# of major spiral chords-early/coiled*	# minor spiral chords early/coiled*	Color of early whorls	Color of late whorls	beading
T. acropora	2	1	3	0	1	3	1	1	1	0	0	2	1	0	0	?	0	3	4	1	0	1
T. altilira	1	1	3	1	0	3	1	1	0	5	2	1	2	1	0	?	0	4	4	?	?	1
T. exoleta	2	0	4	2	1	1	1	1	0	5	1	2	1	1	0	?	0	2	3	0	0	0
T. nodulosa	1	1	2	0	0	3	1	1	1	9	0	1	1	0	0	?	0	4	4	0	1	1
V. bathyalis	?	?	0	1	1	3	1	1	2	3	0	?	1	0	1	0	3	1	0	0	1	0
V. fargoi	?	?	1	1	0	3	1	?	2	3	1	0	1	1	1	3	1	3	4	1	1	1
V. frisbeyae	?	?	4	2	2	2	1	?	1	2	1	?	0	0	1	?	1	2	4	1	1	0
V. gracile	2	0	?	1	2	3	0	0	2	0	0	3	2	0	1	0	3	2	4	0	1	0
V. katiae	0	?	0	2	2	0	0	1	2	9	0	?	1	0	1	1	2	3	1	?	?	0
V. lumbricalis	2	1	0	2	2	3	1	1	1	8	0	2	0	0	1	0	3	2	0	0	1	0
V. milleti	2	?	0	0	2	2	0	0	2	8	0	2	0	0	1	0	2	3	0	?	?	0
V. pellucida	1	1	0	1	1	0	1	0	0	8	1	2	0	0	1	1	2	3	4	0	0	0
V. recta	?	?	0	1	0	3	1	?	2	3	1	0	1	0	1	0	2	4	0	?	?	0
V. spirata	?	?	1	0	1	3	1	?	2	8	1	2	0	1	1	0	2	3	0	1	1	0
V. spirata radicula	?	?	1	0	1	3	1	?	2	8	1	2	0	1	1	2	2	2	0	1	1	1
V. spirata WP	1	?	0	1	2	3	1	1	2	8	0	1	2	1	0	0	0	2	3	0	0	0
V. weberi	?	?	0	1	1	3	1	?	1	1	1	1	2	0	1	2	1	3	1	?	?	0
V. woodringi	1	1	1	2	2	2	0	?	1	2	1	1	0	0	1	1	2	3	4	?	?	0

species	# of major ribs- adult/uncoiled portion*	# of minor ribs, adult/uncoiled portion*	length of uncoiled portion*	coiling axis changes (typical)	lineated appearance on exposed adapical surface	Uncoiled portion wrinkled	Strongest chord early whorls	strongest chord late/uncoiled	hermatypic (with conspecifics)	Turritelline portion umbilicate	coloration pattern	Ventral-Anterior body whorl shape*
T. acropora	3	4	?	0	?	0	2	2	0	0	1	1
T. altilira	2	4	?	0	?	0	3	3	0	0	?	0
T. exoleta	2	3	?	0	?	0	2	0	0	0	1	0
T. nodulosa	4	4	?	0	?	0	2	2	0	0	1	0
V. bathyalis	4	4	2	1	0	1	2	0	0	?	0	?
V. fargoi	4	4	2	1	1	1	3	4	0	1	1	?
V. frisbeyae	?	4	2	1	1	?	3	3	0	1	1	2
V. gracile	0	4	0	0	0	0	2	0	0	?	2	0
V. katiae	4	4	0	0	1	0	2	2	0	1	?	?
V. lumbricalis	1	0	1	1	0	0	3	4	0	0	0	?
V. milleti	1	0	0	1	0	1	4	4	0	0	?	?
V. pellucida	3	4	3	1	1	0	3	3	0	1	0	?
V. recta	4	0	3	1	1	1	3	3	1	0	?	?
V. spirata	4	4	3	1	1	1	3	3	1	0	0	?
V. spirata radicula	4	4	?	1	1	?	3	3	?	0	1	?
V. spirata WP	2	4	?	1	1	?	3	3	0	0	1	2
V. weberi	4	4	2	1	1	0	3	3	0	1	?	?
V. woodringi	3	4	3	1	1	1	3	0	1	1	?	?

Supplemental Tables and Figures for Vermicularia Taxonomy

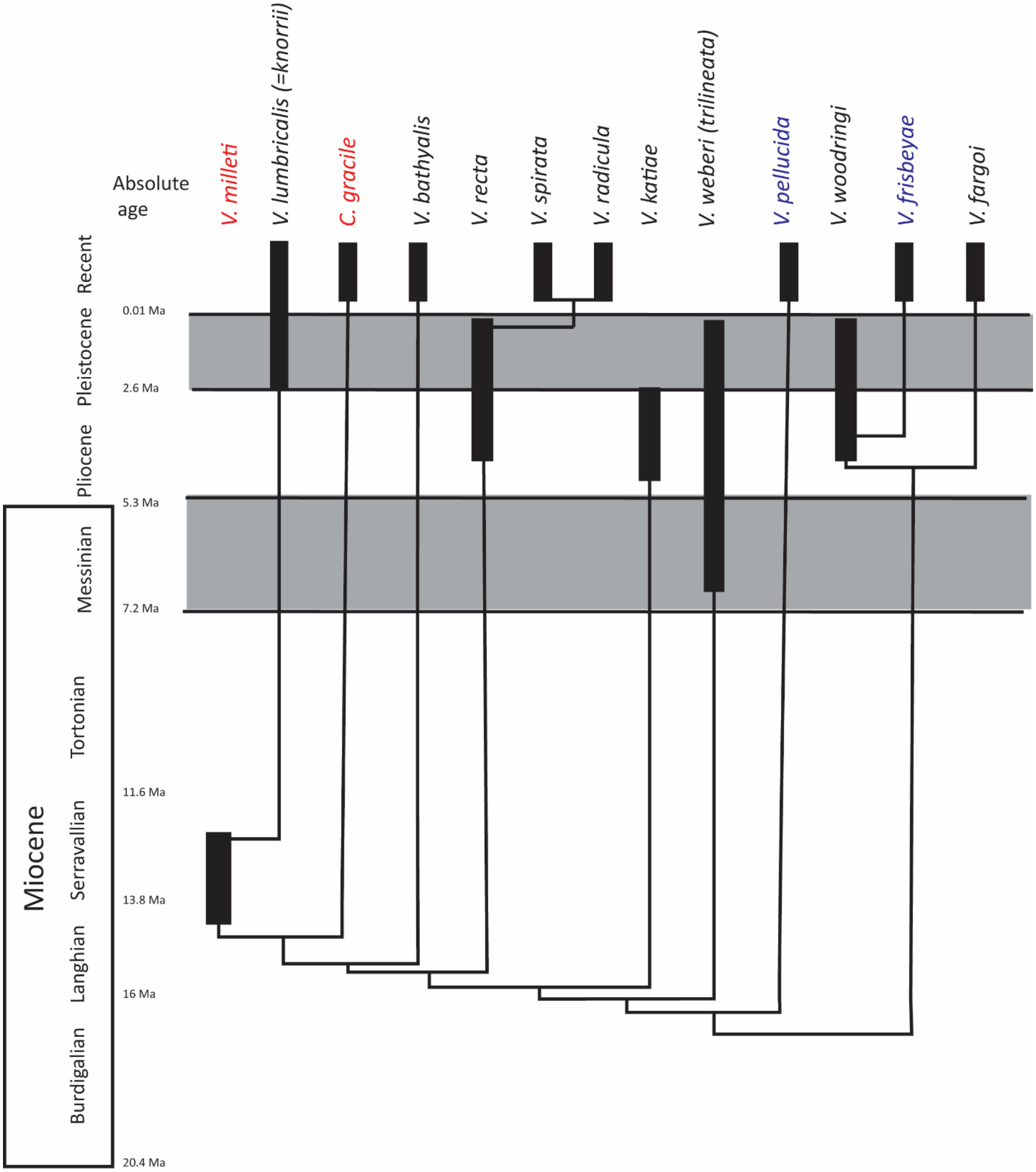


Figure S2.1. Stratigraphic interpretation of parsimony based cladistic result finding *V. milleti* as sister to *V. lumbricalis*. East Atlantic species are in red, Pacific species are in blue, and Western Atlantic species are in black.

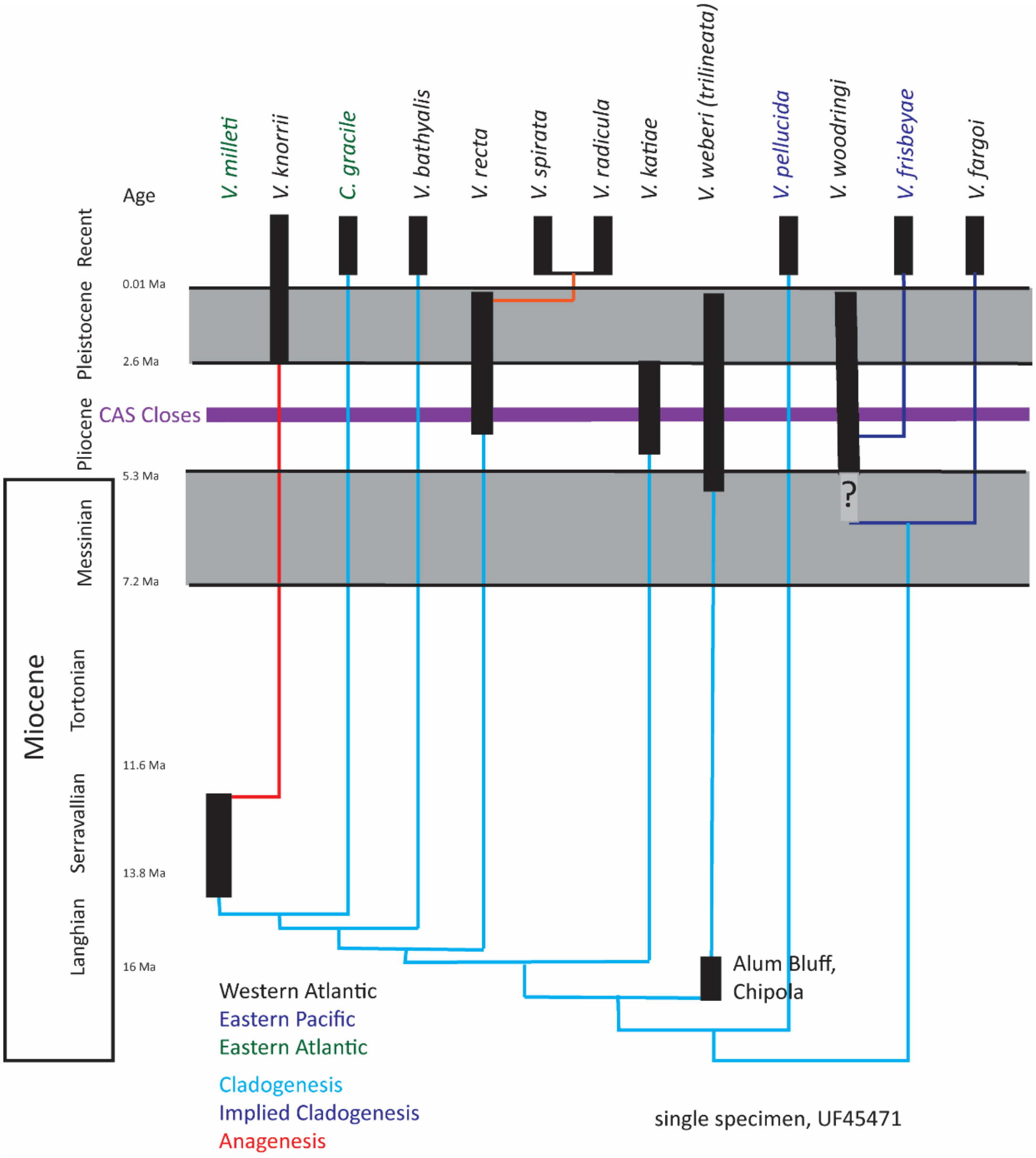


Figure S2.2 Stratigraphic interpretation of the maximum parsimony phylogenetic hypothesis with *V. milleti* as sister to *V. knorrii*, including the Chipola occurrence of *V. weberi* and unconfirmed reports of *V. woodringi* in the late Miocene.

Table. S2.1. Species assigned to Vermiculariinae in error or of unknown affinity.

Species	Author and Year	Proper Assignment	References
V. africana	Cox, 1930	Gastropod, unknown	Bieler and Petit, 2011
V. alternans	Bohm, 1895	Not *Vermicularia* or Vermetid	Bieler and Petit, 2011
V. bezanconi	Cossmann, 1910	Not *Vermicularia*, Vermetid?	Bieler and Petit, 2011
V. bognoriensis	Mantell, 1822	Polychaete	Bieler and Petit, 2011
V. calyculata	von Waldheim, 1807	*Nomen inquirendum*	Bieler and Petit, 2011
V. carinata	Schumacher, 1817	Polychaete	Bieler and Petit, 2011
V. cenomanensis	Gueranger, 1853	Not Vermicularia; Gastropoda	Bieler and Petit, 2011
V. concava	Sowerby, 1814	Polychaete	Bieler and Petit, 2011
V. deposita	Hedley, 1909	Vermetid	Bieler and Petit, 2011
V. flava	Verco, 1907	Polychaete	Bieler and Petit, 2011
V. funicalis	Crespin, 1926	Vermetidae?	Bieler and Petit, 2011
V. fuscata	Humphrey in Jackson, 1937	Unavailable	Bieler and Petit, 2011
V. gorensis	Bosc, 1801	Vermetid	Bieler and Petit, 2011
V. granulata	Gravenhorst, 1831	Vermetid	Bieler and Petit, 2011
V. hindsii	Gray, 1850	Vermetid	Bieler and Petit, 2011
V. intestinalis	Bosc, 1801	*Incertae sedis*	Bieler and Petit, 2011
V. lineolata	Gravenhorst, 1831	Vermetid	Bieler and Petit, 2011
V. manzourensis	Abbass, 1963	Turritellidae; not Vermiculariinae	Bieler and Petit, 2011
V. maoriana	Powell, 1937	Not *Vermicularia; Vermetid?*	Here
V. montensis	Briart and Cornet, 1877	Incertae Sedis, not Vermicularia, not Vermetidae	Bieler and Petit, 2011
V. murayi	Hedley, 1911	Polychaete	Bieler and Petit, 2011

V. nodosa (syn. V. hedleyi)	Hedley, 1907	polychaete	Bieler and Petit, 2011
V. nodus	D'Halloy, 1843	Polychaete	Bieler and Petit, 2011
V. omphalocolpus	Cossmann and Pissarro, 1902	Gastropoda; Not vermetid or Vemicularia	Bieler and Petit, 2011
V. ophiodes	Marshall and Murdoch, 1921	Vermetidae	Biler and Petit, 2011
V. ovata	Sowerby, 1814	Polychaete	Bieler and Petit, 2011
V. panamensis	Chenu, 1846	Incertae sedis; Vermetidae	Bieler and Petit, 2011
V. porrectus	Deshayes, 1861	Vermetid	Bieler and Petit, 2011
V. solariiformis	Cossmann, 1899	Liotiidae	Bieler and Petit, 2011
V. sowerbii	Mantell, 1822	Polychaete	Bieler and Petit, 2011
V. staadii	Cossmann, 1907	Gastropoda; not Vermetidae, not *Vermicularia*	Bieler and Petit, 2011
V. striatus	Reis, 1897	Gastropoda; not *Vermicularia*	Bieler and Petit, 2011
V. torsa	Böhm, 1895	Gastropoda; not *Vermicularia*	Bieler and Petit, 2011
V. tricarinatus	Pethö, 1906	Gastropoda; not *Vermicularia*	Bieler and Petit, 2011
V. umbonata	Sowerby, 1814	Polychaete	Bieler and Petit, 2011
"*Vermicularia* species A" USNM 648498, USNM 648499	Ladd, 1972	Turritellidae; not *Vermicularia*	Here
Genus *Laxispira, including Laxispira gabbi, Laxispira velai*	Wenz, 1939	Siliquariidae	Bandel and Kowalke, 1997; Bieler and Petit, 2011
Genus '*Provermicularia'* (including *Provermicularia circumcarinata)*	Stoppani, 1857; Kittl, 1899	Gastropod, not *Vermicularia;*	Bieler and Petit, 2011
Genus '*Pseuomesalia'*	Douvillé, 1916	Cassiopidae	Kollmann, 1979; Pereira et al., 2016
Subgenus *Anguillospira*	Cossmann, 1912	Siliquariidae?	Bieler and Petit, 2011

Table S2.2: Molecular data included the species sequenced in Sang et al. (in review) (*Lampania cumingi, Batillaria zonalis, Turritella acropora, T. bacillum, T. banksi, T. clarionensis, T. exoleta, T. gonostoma, T. leucostoma, T. nodulosa, T. rubescens* and *T. terebra*) and new sequence data as detailed below.

Species	**Analysis ID**	**Locality**	**Sample ID**
Vermicularia spirata	ESC	Florida	ES1_C04
V. spirata	ESD	Florida	ES1_D04
V. spirata	ESE	Florida	ES1_E04
V. knorrii	BA10	Florida	UF 446833
V. pellucida	BA9	Gulf of Panama	UF 372362
Zaria duplicata	BA1	Bangladesh	PRI private donation
Mesalia brevialis	BA7	Portugal	NHMUK 20030319
Protomella capensis	BA16	South Africa	Natal Museum PO490
Turritella maculata	BA17	Red Sea	PRI private donation
T. communis	BA20	North Sea (Scotland)	NHMUK 20170009
Maoricolpus roseus	BA22	Green Island, Tasmania	Tasmanian museum E35226
Mesalia brevialis	BA35	Spain-Mediterranean	UF 380804
T. nivea	BA38	Senegal	MNHN, IM-2013-63035
Mesalia mesal	BA40	Senegal	MNHN-Paris, IM-2013-63037
T. nivea	BA41	Senegal	MNHN-Paris, IM-2013-63038
Mesalia mesal	BA42	Senegal	MNHN-Paris, IM-2013-63039
T. conspersa	BA43	Senegal	MNHN-Paris, IM-2013-63040
T. conspersa	BA46	Senegal	MNHN-Paris, IM-2013-63043

APPENDIX 3: Supplemental information for chapter 4

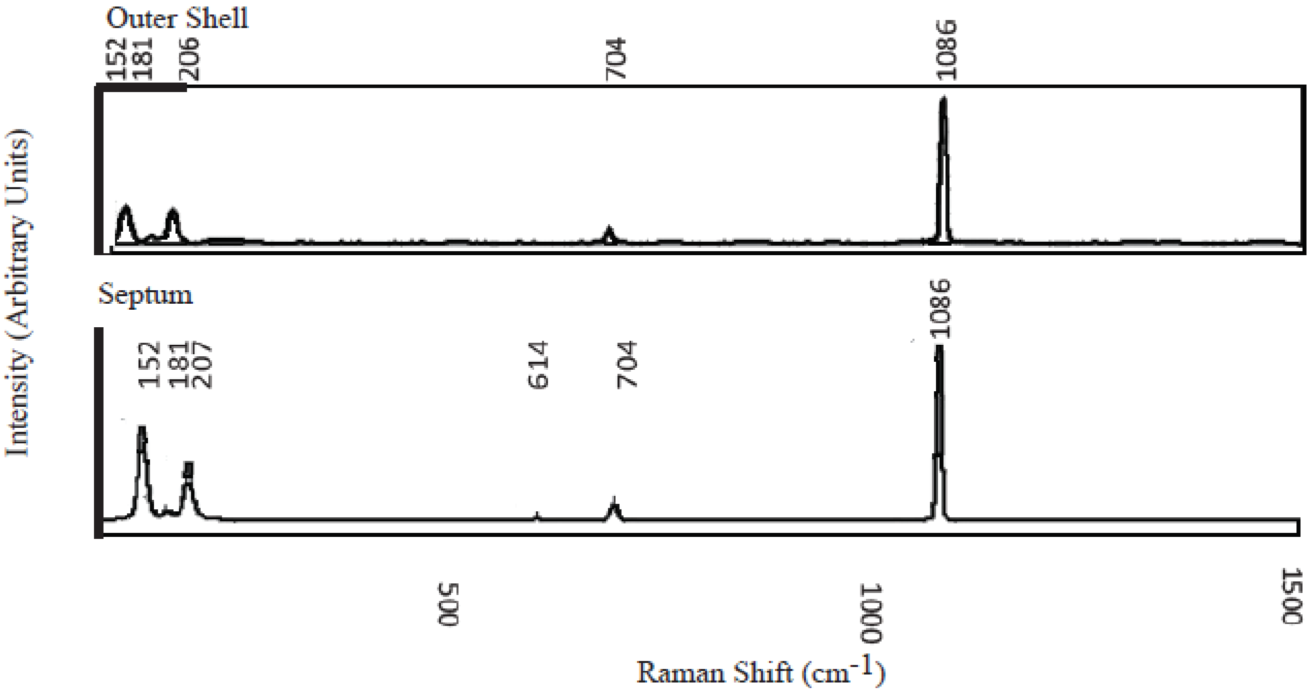


Figure S4.1. Example Raman spectra obtained from *Maoricolpus roseus* outer shell (baseline corrected) and septum. The band at 1086 cm^{-1} is assigned to the v_1 symmetric stretching mode of the carbonate ion. The band at ~704 cm^{-1} is assigned to v_4 in-plane bending, and this band position differs from that observed in calcite, which occurs at 711-714 cm^{-1}. Bands between 152 cm^{-1}and 207 cm^{-1} are assigned to aragonite lattice modes, (calcite lattice modes occur at ~155 cm^{-1} and 281 cm^{-1}) (Frech et al. 1980, Urmos et al. 1991, Wehrmeister et al. 2010).

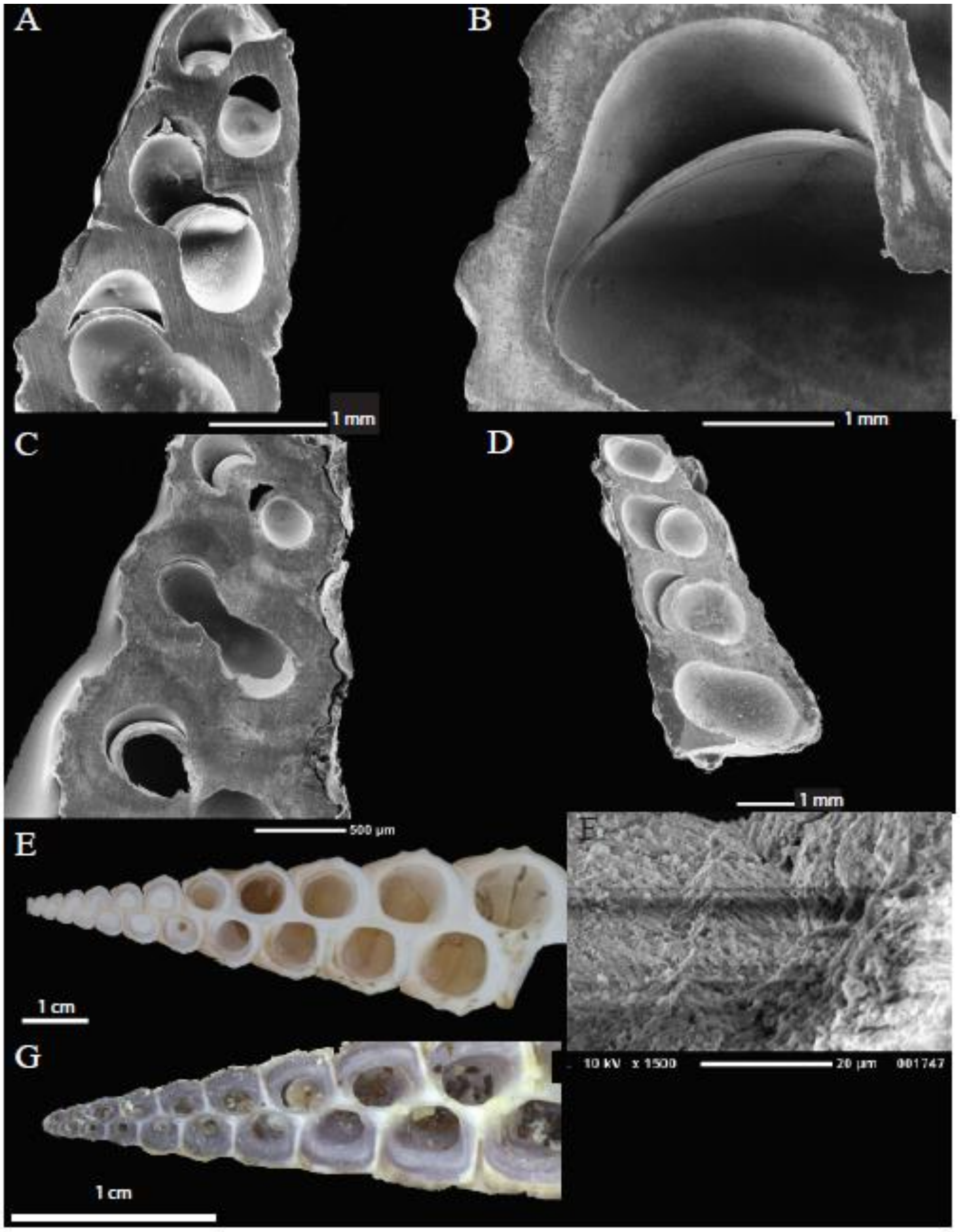


Figure S4.2. Septa observed in various Turritellid genera. A. *Maoricolpus roseus,* SEM B. *Turritella altilira*, SEM C. *T. communis*, SEM D. *Stiracolpus pagoda,* SEM E. *T. duplicata* F. Crossed-lamellar microstructure observed in an incompletely filled apical whorl of the *T. duplicata* specimen shown in E. G. *T. gonostoma.*

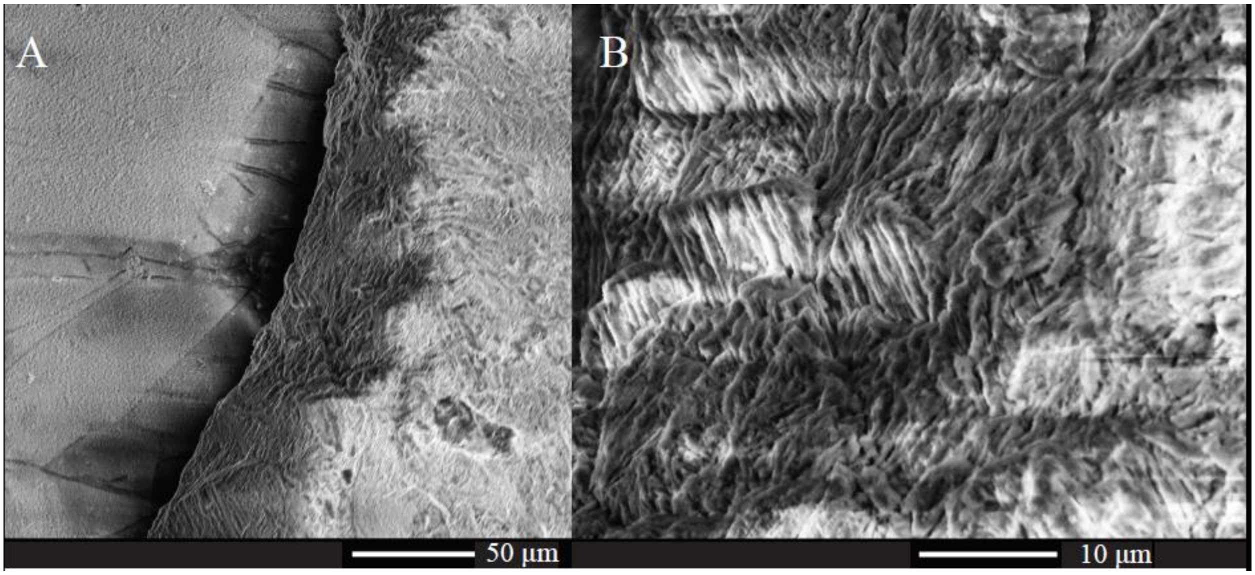


Figure S4.3. SEM images of septa observed in an etched specimen of *Cerithium eburneum*. A. edge of septum showing microstructure. B. Further magnification of septal microstructure.

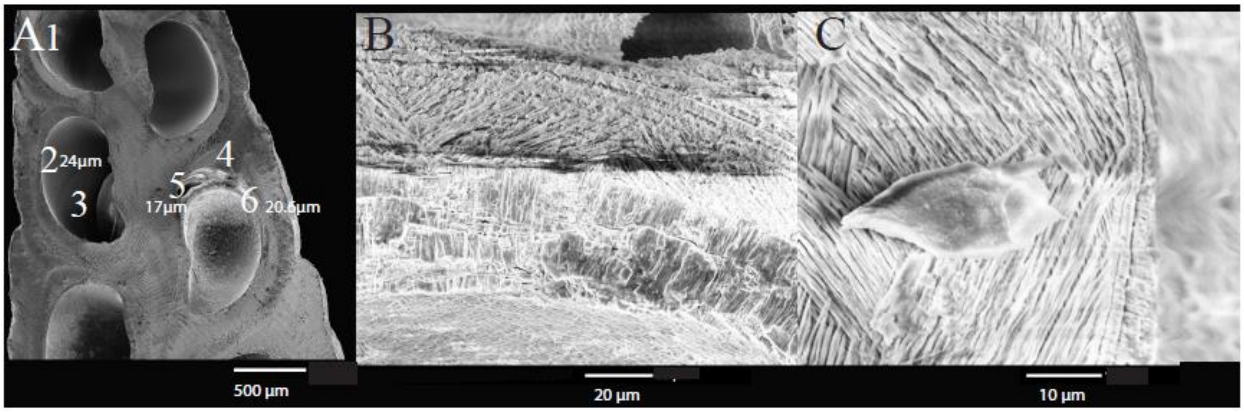


Figure S4.4 SEM images of septa observed in an etched specimen of *Terebra variegata.* A. 6 septa are visible in this image; measurements are provided for 2, 5, and 6 which presented surfaces with orientations indicating true thickness. B. Septal microstructure C. Further magnification of septal microstructure.

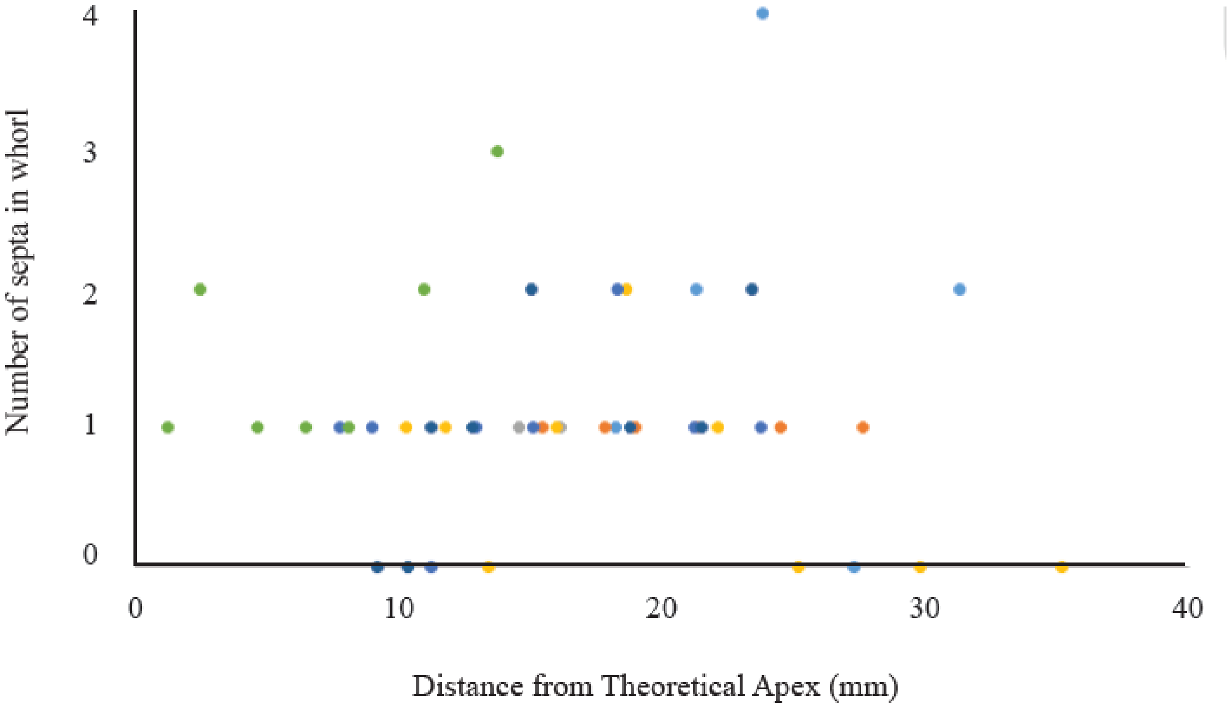


Figure S4.5. Number of septa by distance from the theoretical apex to the midpoint of the whorl examined (Johnson et al., 2017) for 7 *Turritella leucostoma*. Individuals denoted by color.

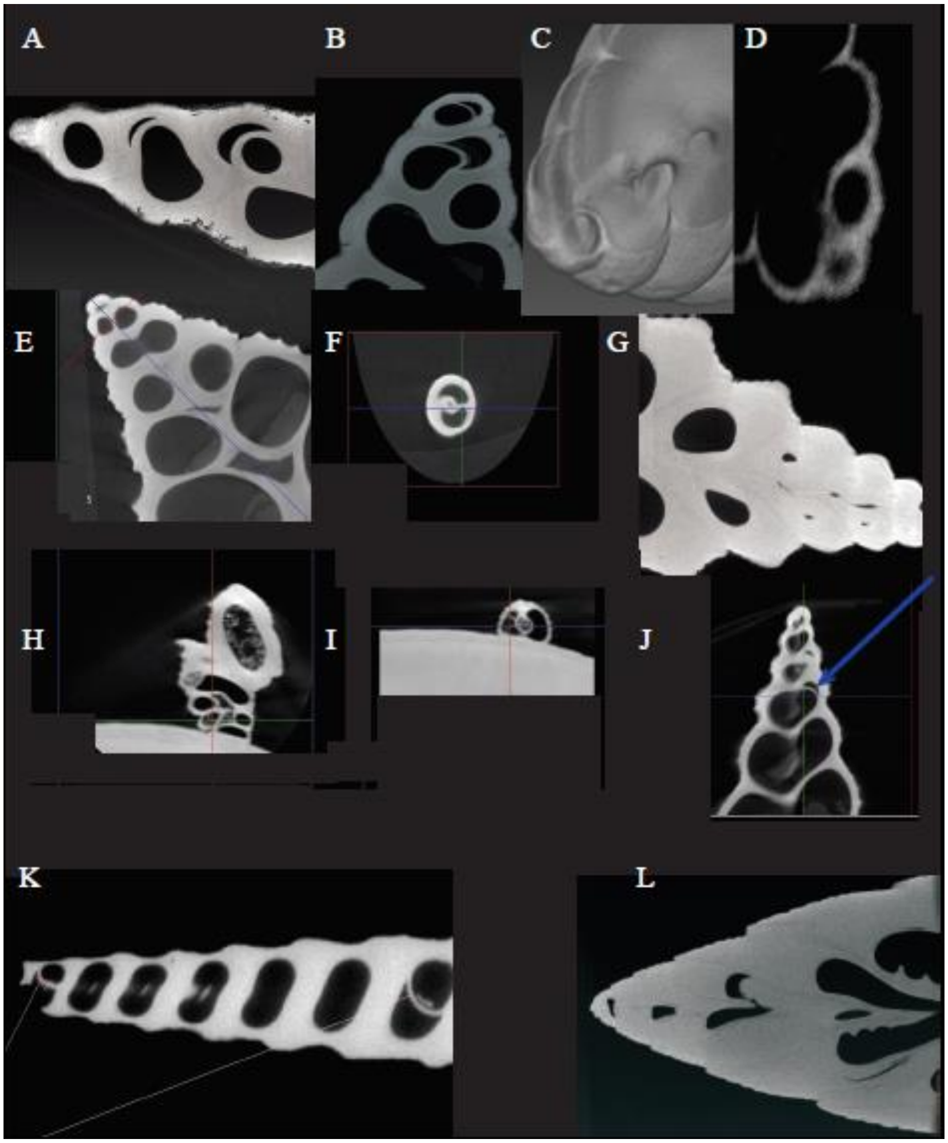


Figure S4.6. CT images from figure 2 showing presence or absence of septa in undamaged specimens of several taxa. A. *Cerithium nodulosum* B. *Opalia* sp. C., D. *Bithynia* sp. E.,F. *Cenchritis muricatus*, G. *Strombus pugilis* H., I. *Petaloconchus complicatus* J. *Nassaria magnifica* K. *Terebra subulata* L *Mitra mitra*

Table S4.1. List of species used in this study and methods employed for observing septa.

Taxon	**Family**	**Observations**	**Citation**	**Catalogue Number**
Pomacea paludosa	Ampullariidae	Direct observation	Observed in this study	PRI 75533
Lampanella sp.	Batillariidae	Direct observation	Observed in this study	PRI 75543
Nassaria magnifica	Buccinidae	Nano-CT	Observed in this study	PRI 75405
Bithynia tentaculata	Bithyniidae	Micro-CT	Observed in this study	PRI 75703
Caecum auriculatum	Caecidae	Literature Reference	[27]	N/A
Campanile symbolicum	Campanilidae	Literature Reference	[26]	N/A
Cerithium eburneum	Cerithiidae	Direct observation; SEM	Observed in this study	PRI 75408
Cerithium nodulosum	Cerithiidae	Nano-CT	Observed in this study	PRI 75406
Opalia wroblewskyi	Epitoniidae	Nano-CT	Observed in this study	PRI 52020
Cenchritis muricatus	Littorinidae	Nano-CT	Observed in this study	PRI 75541
Mitra mitra	Mitridae	Nano-CT	Observed in this study	PRI 75532
Chicoreus brevifrons	Muricidae	Literature Reference	[28]	N/A
Demoulia conglobata	Nassariidae	Literature Reference	[29]	N/A
Segmentorbis sp.	Planorbidae	Literature Reference	[23]	N/A
Pomatias elegans	Pomatiidae	Nano-CT	Observed in this study	PRI 54224
Charonia variegata	Ranellidae	Literature Reference	[28]	N/A
Tenagodus barbadensis	Siliquariidae	Literature Reference	[67]	N/A
Strombus pugilis	Strombidae	Nano-CT	Observed in this study	PRI 10279

Rumina decollata	Subulinidae	Literature Reference	[24]	N/A
Terebra dislocata	Terebridae	Direct observation; measurement	Observed in this study	PRI #s 75398, 75399, 75400, 75401, 75402, 75403
Terebra subulata	Terebridae	Micro-CT	Observed in this study	PRI 75536, 75537
Terebra variegata	Terebridae	Direct observation; SEM	Observed in this study	PRI 68710, 75407
Maoricolpus roseus	Turritellidae	Direct observation; Raman spectroscopy; SEM	Observed in this study	PRI 68538
Stiracolpus pagoda	Turritellidae	Direct observation; measurement; SEM	Observed in this study	PRI 68579
Turritella altilira†	Turritellidae	Direct observation; Nano-CT; SEM	Observed in this study	STRI 17716
Turritella bacillum	Turritellidae	Direct observation; dissection	Observed in this study	Warren Allmon, personal collection
Turritella communis	Turritellidae	Direct observation; measurement; SEM	Observed in this study	PRI 68581
Turritella duplicata	Turritellidae	Direct observation; SEM	Observed in this study	PRI 73078
Turritella gonostoma	Turritellidae	Direct observation; Raman spectroscopy; SEM	Observed in this study	PRI 68541
Turritella leucostoma	Turritellidae	Direct observation; measurement	Observed in this study	Warren Allmon personal collection
Turritella robusta†	Turritellidae	Direct observation; SEM	Observed in this study	STRI 38168
Turritella subannulata†	Turritellidae	Direct observation; measurement; SEM	Observed in this study	PRI 73076
Turritella terebra	Turritellidae	Direct observation; measurement; SEM	Observed in this study	PRI 68583, PRI 68545
Turritella variegata	Turritellidae	Direct observation; measurement; SEM	Observed in this study	PRI 68710, 75407
Vermicularia recta	Turritellidae	Direct observation; SEM	Observed in this study	PRI 73952

Zeacolpus vittatus	Turritellidae	Direct observation; measurement; SEM	Observed in this study	PRI 68585
Petaloconchus complicatus	Vermetidae	Direct observation, Nano-CT	Observed in this study	PRI 75535
Athleta tuomeyi	Volutidae	Literature Reference	[30]	N/A

Table S4.2. Comparison of percent of whorl filled between whorls with and whorls without septa for 6 *Terebra dislocata*. No whorls bore more than 1 septum. Whorl thicknesses measured on side closer to the septum, if a difference was evident.

	N septate/non-septate	Mean % filled, Septum present	Mean % filled, septum absent	t-test p value/ unequal variance t-test p value
Terebra dislocata	2/25	32.2	23.4	0.0101/0.0044

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